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Behavioural models of penguins and krill in the Southern Ocean

A thesis submitted in accordance with the requirements of the Open University for the degree of

Doctor of Philosophy

by

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March 2006

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ABSTRACT

The thesis applies state of the art ecological modelling methods to predict optimal behavioural patterns in two key Southern Ocean species, macaroni penguins, *Eudyptes chrysolophus*, and Antarctic krill, *Euphausia superba*. The work is divided into three main parts. The first considers how female macaroni penguins allocate their time between searching, foraging and feeding their chick during the guard stage. The model is forced by the availability of their main prey, Antarctic krill, and the increasing demands of the chick. The second part focuses on the behaviour of Antarctic krill at South Georgia, a hotspot in the Southern Ocean. This model predicts the most likely distribution of krill between 3 main environments that relate to bathymetry, resulting from an individual's choice of depth, density of swarm and swimming behaviour, which has some influence on their advection. The model is forced by the availability of phytoplankton and by the prevailing advection regime. The third part takes a similar approach, determining the optimal behaviour of krill as they are transported from the Antarctic Peninsula to South Georgia, except in this model, krill do not have any influence on their horizontal location. The first main finding of the thesis is that macaroni penguins will travel further to obtain a more reliable meal of krill, even if the krill reward does not change with distance from nest. A second important finding is that krill are able to increase their overall concentration in favourable areas simply by altering their swimming speed and turn rate. The third major finding describes the likely existence of a threshold availability of krill to penguins, below which the chick dies and above which there is no change to chick growth. The thesis discusses the suitability of the modelling technique and proposes future fieldwork for better model parameterisation and validation. The models provide a framework for predicting the responses of these organisms to future changes in their environment.

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1.

General Overview

INTRODUCTION

The Southern Ocean

The Southern Ocean is a crucial component of the global marine ecosystem, covering an area around 10% of the world's oceans (Constable et al., 2003). The main current here is the Antarctic Circumpolar Current (ACC), which runs eastward unbroken around the globe (Constable et al., 2003; Foster, 1984; Orsi et al., 1995). The ACC is the world's strongest current, transporting more water than any other, extending 200 to 1000 km wide and reaching the ocean floor (Foster, 1984; Orsi et al., 1995; Whitworth et al., 1982). The unbroken movement of the ACC creates the Polar Front, a biological barrier that separates the distinct physical and biological regimes of the Southern Ocean from those to the north (Constable et al., 2003; Foster, 1984).

A number of factors contribute to the uniqueness of the Southern Ocean, sparking interest in both research and exploitation here. Firstly, primary productivity within the ACC is highly variable despite generally high nutrient conditions (Martin, 1990; Minas and Minas, 1992; Ward et al., 2002). Maximum phytoplankton biomass is relatively low because of a combination of low temperatures, micronutrient limitation, high microplankton grazing pressure and high wind stress that leads to deep mixing over much of the region (Ward et al., 2002). However frontal regions often support higher levels of production compared to the surrounding oceans (Boyd et al., 1995; Korb et al.,

2004). The frontal regions may be the reason that the Southern Ocean is able to support such an extensive number and array of vertebrate predators.

South Georgia and the Scotia Sea

South Georgia is a narrow, mountainous island in the southwest Atlantic Ocean, with a broad continental shelf (Atkinson et al., 2001; Brandon et al., 2000). Although mid-latitude, the island is south of the Polar Front, heavily glaciated, and considered polar in both the local environment and extensive food web it supports (Gordon et al., 1977; Orsi et al., 1995; Trathan et al., 1997). Productivity in the ocean around South Georgia is characteristically much higher than in the rest of the Southern Ocean in terms of phytoplankton and zooplankton biomass, with a particularly high biomass of Antarctic krill, *Euphausia superba*, and land-based krill-predators such as penguins and seals (Atkinson et al., 2001; Boyd, 2002b; Croxall and Prince, 1979; Korb et al., 2004). The biomass of phytoplankton and krill are highly variable from year to year, with the effects manifesting themselves in the condition, diet and breeding success of krill predators (Atkinson et al., 2001; Croxall et al., 1999; Murphy et al., 1998; Trathan et al., In Press). A long history of exploitation has caused additional perturbation in the ecology of the region.

Exploitation began in the late 18th and early 19th century, when the harvesting of fur seals left the population very near to extinction at South Georgia, and elsewhere in the South Atlantic (Mori and Butterworth, 2005; Payne, 1977a). From the start of the 20th century, there was a sequential harvesting of whale species, such that: Antarctic blue whales, *Balaenoptera musculus*, were hunted to less than 0.5% of pre-exploitation levels; fin whales, *Balaenoptera physalus* were heavily impacted; humpback whales,

Megaptera novaengliae, were reduced to around 1 to 5% of their previous levels; as were sperm whales, *Physeter macrocephalus*, and sei whales, *Balaenoptera borealis* (Mori and Butterworth, 2005). In the early 1970s, harvesting had a dramatic effect on a number of finfish species, with the near disappearance of the Antarctic rockcod, *Notothenia rossii*, after 514000 tonnes were taken from South Georgia, and most recently, the targeting of some stocks of the Patagonian toothfish, *Dissostichus eleginoides*, due in part to illegal fishing, have led to critical bycatch issues for some species of albatrosses, petrels, skates and rays (Brandao et al., 2002; Constable et al., 2000). Finally, Antarctic krill has been harvested since the late 1960s (Everson and Goss, 1991), with catches in the Scotia Sea over the last 10 years stable at around 100 000 tonnes a year (Mori and Butterworth, 2005; Nicol and Foster, 2003). This level is much lower than the precautionary catch limit specified by CCLAMR of 4 million tonnes and the full impact of reaching such a limit remains uncertain (Mori and Butterworth, 2005; Trathan et al., 1995). In addition, natural variability and regional effects mean that even a smaller catch can affect predators if close to an island during the breeding season.

Despite the negative impacts of harvesting, it was actually an attempt to sustain the southern whale fishery that spawned the pioneer works of the Discovery Committee in the 1920s and 1930s and set the beginnings of our knowledge about krill biology and distribution (Foster, 1984; Godlewska, 1996; Kemp et al., 1929; Mackintosh, 1972; Marr, 1962; Quetin et al., 1994). The *Discovery Investigations* took an ecosystem approach, aiming to understand the causes of the high primary productivity and how it was linked to fisheries (Atkinson et al., 2001). Between 1940 and 1970 there was little scientific work at South Georgia, and interest in the area re-emerged in the 1970s as

concern increased about the exhaustion of shelf fishing grounds (Atkinson et al., 2001; Godlewska, 1996). The establishment of a krill fishery around this time was also cause for concern, prompting the establishment of an international programme of Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) in the early 1980s (El-Sayed, 1994). BIOMASS was targeted primarily at krill research. Additional measures have been taken to prevent the repetition or continuance of severe exploitation, with the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) introduced in 1982 (Boyd, 2002b). Given the history and ecological significance of this region, continued research on species interactions and future effects of harvesting has fundamental importance.

Krill

It has long been recognised that Antarctic krill are central to Antarctic food webs, with many organisms either predating directly on krill or being just one trophic level removed (Fraser, 1936; Mangel and Nicol, 2000; Marr, 1962). In addition to their central role in the Antarctic ecosystem, there are a number of reasons why krill are so well studied. Firstly, they are among the world's most abundant metazoan species (Nicol, 1994), with estimates that current populations of whales, birds, pinnipeds, fish, and squid consume 250 million tonnes of Antarctic krill annually (Hamner and Hamner, 2000; Miller and Hampton, 1989). Secondly, krill are long-lived and the largest pelagic crustacean (Nicol, 2003), reaching a maximum size of around 60 mm in approximately 5 years (Quetin et al., 1994; Siegel, 1986). Thirdly, krill can shrink under unfavourable conditions; a unique aspect of their growth that is not observed in many organisms and makes them inherently flexible to variable and challenging conditions (Hofmann and Lascara, 2000; Ikeda and Dixon, 1982; Marinovic and Mangel, 1999; Nicol et al.,

1992). As a resource, krill are variable as well, in terms of their depth in the water column due to diel vertical migration (DVM) (Godlewska, 1996; Kalinowski, 1978), their ability to form polarized schools, affecting their density and patchiness (Hamner and Hamner, 2000; Marr, 1962; Ritz, 1994), and their strong swimming capacity, that can affect their advection and retention depending on the currents in particular areas (Kils, 1981; Murphy et al., 2004a). The recent establishment of a krill fishery has sparked additional research into the potential effects of fishing on krill and krill predators, with particular concern about what might happen if the catch rate increases (Croll and Tershy, 1998; Mangel and Switzer, 1998). A long-term decline in krill stocks, by as much as 80% over the last 30 years, due most likely to the declining extent of sea-ice, has raised concern about krill numbers (Atkinson et al., 2004).

Macaroni penguins

Macaroni penguins, *Eudyptes chrysolophus*, are the most abundant penguin species in the world, and play an important role in sub-Antarctic oceans around the globe (Barlow and Croxall, 2002b; Woehler, 1993; Woehler and Croxall, 1997). During the summer breeding season, these birds are constrained in high numbers to islands and become particularly reliant on krill as their main food source (Barlow and Croxall, 2002b; Croxall et al., 1997; Trathan et al., 1998). At South Georgia, macaroni penguins may consume around 8 million tonnes of krill annually (Boyd, 2002a), with much of this concentrated in the breeding season when their foraging range is constrained by a need to return to the nest. The impact of these predators on the surrounding oceans during the breeding season is therefore high, which highlights the importance of understanding their foraging behaviour and effect on krill at this time of year. In addition, the last two or three decades have seen the decline of population numbers of macaroni penguins at

South Georgia (Ellis et al., 1998; Trathan et al., 1998). This may be related to a rapid increase in the sympatric predator, the Antarctic fur seal, *Arctocephalus gazella* (Barlow et al., 2002; Bonner, 1968; Headland, 1984), which also feeds on Antarctic krill and breed at South Georgia around the same time of year as macaroni penguins (Croxall et al., 1999; Reid and Arnould, 1996). The population of fur seals has increased rapidly since the 1950s, recovering from virtual extinction during the first half of the 19th century (Barlow et al., 2002; Payne, 1977b). It is plausible that the increase in fur seals has led to a decrease in penguin numbers, but it is not clear whether this is because they are reducing the level of food available or because they are reducing the available breeding area. This is a classic example of an upset in the ecosystem due to exploitation, affecting the populations of two key species. It highlights the importance of understanding the interactions between species, particularly the key factors determining foraging behaviour during the breeding season.

Brief Antarctic summer

The brief Antarctic summer is an important time of year for both krill and their predators. This time of year, including late spring, is when the majority of krill spawning occurs, mostly around the Antarctic Peninsula (Bargmann, 1945; Marr, 1962). This is also the time of most rapid juvenile growth, due to phytoplankton blooms associated with the retreat of the sea-ice (Atkinson et al., In Press). Reasons for increased production in the marginal ice zone include: the establishment of a stable layer at the ocean's surface due to low density fresh water from the melting ice, allowing phytoplankton to grow in a well-illuminated environment; a decrease in turbulence within the mixed layer caused by reduced wind stress from the presence of ice; and the release of ice algae into surface water from melting ice floes (Smith and

Nelson, 1986). This is also the time of year when a proportion of krill are believed to begin a significant journey from their place of spawning, at the Antarctic Peninsula, across the Scotia Sea to South Georgia (Fach et al., 2002; Hofmann et al., 1998; Mackintosh, 1973; Marr, 1962; Murphy et al., 1998). Although conditions generally support a higher phytoplankton abundance than the rest of the year, the availability of phytoplankton is also highly variable, and generally still low across the Scotia Sea (Korb et al., In press). It is important to determine how krill respond to this variability in terms of their behaviour and growth, which will in turn affect their availability to predators.

Summer means the breeding season for a number of krill-predators based on islands across the Scotia Sea (Croxall et al., 1988b). Predators are constrained at this time with a need to find sufficient prey, krill, within a restricted range from their breeding sites, resulting in a number of interesting interactions between predators and krill at this time of year. In addition, the occurrence of years where krill are in low supply have been linked to breeding failure, or reduced success, in many krill-reliant predators (Croxall et al., 1999; Everson et al., 1997; Kock et al., 1994; Lynnes et al., 2004; Murphy et al., 1998), highlighting their sensitivity to changes in krill availability and distribution at this time.

Models and behaviour

The use of models in ecological studies has a number of benefits. Models can provide direction for future field experiments, the results of which can provide feedback to improve or inspire the creation of more accurate models (Werner, 1992). In addition, models allow scenario testing in situations where fieldwork is not viable. In the testing

of a model it is also possible to ascertain weaknesses in the data, where further field experiments are required. Finally, the use of models in behavioural ecology allows the prediction of how organisms may respond to future scenarios, such as climate change, or shifts in the extent of sea-ice.

Population and community ecology has traditionally relied on mathematical models that essentially ignore behaviour, such as the Lotka-Volterra models of predation and competition, in which population densities are the only dynamic variables (Abrams, 1995; Werner, 1992). However, there is a general understanding among ecologists that behaviour is critical to the specification of interactions between species (Werner, 1992). Particular behaviours determine the nature and magnitude of interactions, be they among competitors, mutualists, parasites and their hosts, or predators and prey (Werner, 1992). A growing number of studies show that changes in interaction-related traits has a major effect on species abundances and/or growth rates (Fraser and Gilliam, 1992; Power, 1987). In addition, a large number of behavioural ecology studies demonstrate adaptive alterations in behaviour of animals to various factors (Krebs and Davies, 1984) and especially to the presence of predators (Lima and Dill, 1990), highlighting the importance of behaviour in models of the ecosystem.

Predator-prey dynamics are a relatively well-studied example of interactions between individuals that have population- and community- level consequences (Alonzo, 2002). Two main approaches have been used to study predator-prey interactions: the population dynamics approach; and the optimal foraging and habitat selection research that has focussed mainly on individual behaviour (Alonzo, 2002). Lima (2002) has argued for a need to put predators back into behavioural predator-prey interactions.

Although many population models exist, they tend to assume fixed or extremely simple predator and prey behaviours while focusing on predicting population dynamics (Alonzo, 2002). Other research has concentrated on individual foraging behaviour and habitat selection (Clark and Mangel, 2000; Houston and McNamara, 1999; Mangel and Clark, 1988), but mainly ignoring the interaction between species. Game theory takes this further to examine the interaction between species, but is constrained by a need for simple models because of the great computing power needed. This thesis considers the foraging decisions of both the predator and prey (although not simultaneously like game theory) in an attempt to gain a better understanding of the interaction between species at South Georgia.

Dynamic state variable modelling

Stochastic dynamic programming (SDP) models (otherwise called dynamic state variable models) are a mathematical approach to decision theory, using a programming algorithm for solving complex, stochastic, state-dependent optimisation problems that are generally impossible to analyse and understand within a purely analytical framework (Hutchinson and McNamara, 2000; Shea and Possingham, 2000). Invented in the 1950s by Richard Bellman, a mathematician, dynamic programming has a long history in economics and engineering (Bellman, 1957; Intriligator, 1971). Mangel and Clark (1986) and McNamara and Houston (1986) were first to employ the technique to problems of behavioural ecology in the 1980s. Since then, SDP modelling has been applied to a number of problems, including: foraging, from diel foraging patterns in small birds (Houston and McNamara, 1993; McNamara and Houston, 1987; Thomas, 2000) to variations in foraging patterns in limpets (Burrows et al., 2000); migration of birds to and from breeding grounds (Clark and Butler, 1999; Farmer and Wiens, 1999;

Weber et al., 1998); the vertical distribution of zooplankton in the water column (Alonzo and Mangel, 2001; Fiksen, 1997a; Fiksen and Carlotti, 1998; Fiksen et al., 2005; Fiksen and Giske, 1995; Titelman and Fiksen, 2004); mating behaviour (Alonzo and Warner, 2000; Lucas and Howard, 1995; Sih, 1994); and many other scenarios (Clark and Mangel, 2000; Houston and McNamara, 1999; Mangel and Clark, 1988). Models of this type examine which behaviour patterns are optimal for individuals within a set of constraints, and are particularly well suited to empirical studies based on field or laboratory data (Clark and Mangel, 2000).

In a dynamic state variable model, the individual chooses an action at each discrete time step. The action may be behavioural, such as foraging or moving, or physiological, such as moulting (Hutchinson and McNamara, 2000). The action chosen depends on the state of the individual, and affects both a measure of its fitness and its state in the next interval. Characterisation of state can include an individual's energy reserves, its size, the number of its dependent offspring, environmental variables such as temperature or prey density, or other factors, including predation (Clark and Mangel, 2000; Houston and McNamara, 1999; Hutchinson and McNamara, 2000; Mangel and Clark, 1988). The state of an individual can constrain its possible actions; for example, the amount of prey items collected by a bird may limit its clutch size (Bolton et al., 1992), and likewise, the energy stored by a female Antarctic krill can determine the number of spawning events in a season (Nicol et al., 1995).

In these types of models, fitness is frequently defined as the expected reproductive success from a specified time until the end of the individual's life, which in life-history theory is denoted R_0 (Clark and Mangel, 2000; Roff, 1992; Stearns, 1992). This means

that fitness is defined in terms of current and future reproductive success (Clark and Mangel, 2000). This is based on the assumption from evolutionary theory that alleles in individuals with superior reproductive rate will increase their representation in future generations (Stearns and Schmid-Hempel, 1987). Therefore, factors defining fitness are those that affect the future reproductive success of an individual; such as long-term survival, number of offspring, or energy reserves (Fiksen, 1997b; Hutchinson and McNamara, 2000).

The development of an SDP model firstly requires characterisation of the discrete time interval and basic time horizon. The length of each time step should be set according to the total amount of time that the model is covering (Clark and Mangel, 2000). This can depend also on the speed of the computer; for example, it might be unrealistic to model behavioural decisions made every second for an entire year, but to instead consider a time step of one or two weeks. The state variables and constraints must also be defined, for example, as an individual's energy reserves, constrained by a maximum stomach size. Next, the model requires a definition of the decision or action variables, such as foraging, followed by the state dynamics, such as how the individual's energy reserves increase with foraging. The final factor to be considered is fitness and the terminal fitness function, to determine, for example, if the individual is to maximise survival or number of offspring in the long-term (Clark and Mangel, 2000).

The dynamic programming itself works backward in time to calculate the optimal 'policy' for each level of the state variables of the individual and for each discrete unit of time (Clark and Mangel, 2000; Houston and McNamara, 1999; Mangel and Clark, 1988). The optimal policy specifies that action or decision that maximises fitness for

each state at each time. Moving forward through the time steps, an individual with an initial set of state parameters effectively has a map of the optimal decisions to make at each time step, which will further affect its state and fitness and therefore the decision chosen at the following time step. Adding a measure of stochasticity to the state dynamics, for example the outcome of a foraging event, means that the behavioural routine over time will vary between individuals even though they are using the same optimal policy.

AIMS

The aims of this thesis are to examine the behavioural decisions made by two key species in the Southern Ocean ecosystem by the application of a state of the art modelling approach. Up to date parameters will be used for all of the models, with the aim of identifying potential interactions between macaroni penguins and krill at South Georgia and in the Scotia Sea. I also aim to make predictions of how behaviour and interactions will change under certain future scenarios, such as climate change, and to provide testable hypotheses for future validation through fieldwork or other models. Finally, the aim of the modelling technique will be to identify areas requiring improved levels of parameterisation through field observations or laboratory studies.

The work is split into three main models. The first model considers how adult penguins allocate time between searching, foraging and feeding the chick during the guard stage of the breeding season at South Georgia, with the parent responding to variable prey conditions and the increasing demands of the chick. The availability of prey is the forcing function of this model, and is varied to simulate a number of scenarios including good and bad krill years. The second model will examine the behaviour of krill at

South Georgia, which has particularly high levels of krill-predators and phytoplankton (the principle food item of krill). This model gives the small-scale response of krill behaviour to variable levels of food, oceanographic currents and predation from land-based predators. Krill behaviour varies in this model in terms of depth, density of swarming and swimming behaviour. The third model takes a similar approach, determining optimal behaviour patterns of krill as they are advected from the Antarctic Peninsula to South Georgia. However, rather than horizontal migration being a behavioural response in this model, it is predetermined by predicted drifter and model tracks. The krill behavioural response in this model is measured in terms of vertical migration and swarming behaviour, and is forced by food availability and distance to the nearest predator colony.

2.

Optimal behavioural decisions of macaroni penguins during the guard stage

INTRODUCTION

Macaroni penguins are the most abundant penguin species in the world (Barlow and Croxall, 2002b; Woehler, 1993; Woehler and Croxall, 1997). They concentrate on a number of sub-Antarctic islands throughout the Southern Ocean during the austral summer in order to breed (Williams, 1995). Population numbers on these islands can be up to several million pairs during this time, and their impact on the structure and function of the surrounding ecosystems is high. Their high demand for prey means that they are sensitive to prey availability during the breeding season, particularly with respect to breeding success (Atkinson et al., 2001; Croxall et al., 1999; Reid et al., 2002). Understanding the foraging behaviour of this species is therefore a crucial part of being able to predict how they may respond to future environmental changes and in the context of fisheries that compete for the same resource (Barlow and Croxall, 2002b; Green et al., 2005).

One of the island archipelagos where macaroni penguins are most abundant is South Georgia, where an estimated 2.5 million pairs breed each summer (Barlow and Croxall, 2002b; Trathan et al., 1998). South Georgia is a sub-Antarctic island in the southwest Atlantic Ocean and, since its discovery, has been recognised as an important biological

site, leading to significant research and exploitation in the region (Atkinson et al., 2001; Everson and Goss, 1991; Marr, 1962). The South Georgia region is characterised by a high biomass and productivity of phytoplankton, zooplankton and vertebrate predators, with a particularly high biomass of Antarctic krill, which make up over half the total zooplankton biomass in the region (Atkinson et al., 2001). During the breeding season, macaroni penguins at South Georgia are believed to rely almost exclusively on Antarctic krill as their prey (Croxall et al., 1997). However, as a resource, krill are patchy in space and time, with the occurrence of ‘bad’ krill years (years of significantly low krill concentrations) often resulting in nest failure or decreased offspring weight for macaroni penguin chicks and other krill-reliant predators, such as Antarctic fur seals (Atkinson et al., 2001; Croxall et al., 1999; Reid et al., 2002).

There are a number of reasons why krill availability is so variable. Firstly, the fact that krill are located in swarms, of varying degrees of density, affects their patchiness (Ritz, 1994), and diel vertical migration affects their depth in the water column at any time (Godlewski, 1996). Secondly, there is notable interannual variability in the general population dynamics of krill, and rates of mortality, recruitment and breeding success can vary by large degrees (Siegel, 2000a). Thirdly, physical factors can have a large effect on local abundance, with transportation by ocean currents constantly moving krill in and out of specific regions (Murphy et al., 2004b) and year to year variations in sea-ice extent influencing distribution and survivorship (Atkinson et al., 2004). Finally, the last 30 years have seen the development of a fishery for Antarctic krill in the Southern Ocean (Atkinson et al., 2001; Everson and Goss, 1991; Mangel and Switzer, 1998), and there is concern about its indirect effects on krill-reliant predators, such as macaroni penguins, in affected regions (Mangel and Switzer, 1998).

The breeding season for macaroni penguins spans around 6 months (Williams and Croxall, 1991). During this time, both parents undertake various duties to raise a single chick to the point where it can leave the island before the onset of winter (Davis et al., 1989). The correct timing of the different breeding events is important. The breeding cycle begins with courtship in November, followed by incubation in December, when parents alternate long foraging trips with long periods of sitting and incubating the egg (Barlow and Croxall, 2002b; Williams and Croxall, 1991). January is the guard stage, where the male sits guarding the newly hatched chick while the female undertakes a number of short foraging trips to bring back meals for the chick (Barlow and Croxall, 2002b; Williams and Croxall, 1991). This is followed by the crèche period, when both the male and female return to the nest with meals for the chick, which is now large enough to gain protection by joining a crèche of fellow chicks (Barlow and Croxall, 2002b; Williams and Croxall, 1991). After this stage, the parents return to sea and the chick fledges (Barlow and Croxall, 2002b). The guard stage, lasting 23 days, is perhaps when the female is under the most pressure, since she must provide regular and constantly increasing meals for the rapidly growing chick (Williams, 1982). Although continuously foraging, she loses on average 14% of her body weight during this stage, with the fasting male losing on average 25% (Barlow and Croxall, 2002a). This is also the stage when female desertion is most likely, resulting in possible nest failure (Barlow and Croxall, 2002a). The decisions made by the female at this time are therefore crucial to a successful chick rearing, and these decisions are likely to be most sensitive to changes in krill availability and distribution.

Provisioning behaviour is an important aspect of parental expenditure, which is defined as the resource allocated to offspring care, including time and energy (Barlow and Croxall, 2002a). Long-lived seabirds such as macaroni penguins are expected to maximise lifetime reproductive success, which includes the trade-off between reproductive expenditure one year and potential future reproductive output (Barlow and Croxall, 2002a; Green et al., 2002; Varpe et al., 2004). Therefore, during chick rearing, the female is constrained by the need to deliver food to the chick, but also to maintain her own body condition, which results in shorter trips at this time of breeding compared to incubation (Barlow and Croxall, 2002b; Green et al., 2005). As well as a need to maximise food intake and minimise time away from the chick, the foraging decisions of the female may vary according to light, presence of sea-ice, prey abundance and variability, breeding stage and energy demands (Jansen et al., 1998; Tremblay and Cherel, 2003). While there are some general observations on variability in foraging trips through the different stages of the breeding season (Barlow and Croxall, 2002b; Green et al., 2002; Trathan et al., 1998) and on chick failure in years of low krill availability (Barlow and Croxall, 2002a; Irvine et al., 2000), there is little work on variation in foraging behaviour in response to changing conditions. This is where a dynamic state variable model can offer some insight.

The foraging behaviour of penguins is difficult to observe, because while at sea they are cryptic and difficult to follow. However, miniature electronic devices have recently provided a means to study seabird foraging behaviour in the field (Wilson et al., 2002). Instruments include: time-depth-recorders (Cherel et al., 1999); radio tracking (Wanless et al., 1993); and most recently, satellite telemetry (Barlow et al., 2002; Barlow and Croxall, 2002b; Trathan et al., 1998). In this way, it is now possible to determine the

foraging trip duration and range, and depth of foraging dives. Although there are only a small number of studies using satellite tracking, some general patterns have already emerged from these. For macaroni penguins, there are noticeable differences in foraging trip duration between sexes, between stages of the breeding season, and within stages of the breeding season. For example, trips during incubation tend to be longer and further from the nest than trips during chick rearing (Barlow and Croxall, 2002b). In addition, there is evidence that macaroni and Adélie penguins, *Pygoscelis adeliae*, may take longer trips towards the end of the guard stage (Croxall et al., 1993; Kato et al., 2003 but see Green et al., 1998). At present, there is little understanding on what is driving these changes in foraging strategy although it is likely that the changing balance of trade-offs is a major driver.

Dynamic state variable models have proven very successful in understanding the trade-offs involved with energy reserve management in general, including under the influence of food supply, metabolic costs, predation risk and social interactions (Clark and Mangel, 2000; Mangel and Clark, 1988). These type of models are valuable for analysing the effects of environmental stochasticity on life-history strategies (Houston and McNamara, 1999), and further, in the context of caring for dependent young (Beauchamp et al., 1991; Welham and Beauchamp, 1997; Winkler and Adler, 1996). The model by Beauchamp *et al.* (1991) investigates food allocation to starlings, *Sturnus vulgaris*, considering the effects on future and current reproductive success. Welham and Beauchamp (1997) investigate the relative performance of different provisioning currencies and a state dynamic model for black terns, *Chlidonias niger*. The results from their study suggested that both the state variable model and the model maximising efficiency produced the highest fitness returns (Welham and Beauchamp, 1997). Their

model considered chick condition as a state variable, although the fact that its energy demand increases with age was not considered.. The state dynamic model presented by Winkler and Adler (1996) investigates the changing chick demands in detail, but is only a sub model and does not examine parental foraging trips. A further study investigates the trade-off between parental and offspring state under energetic risk and how it is influenced by residual reproductive values (Dall and Boyd, 2002). The main result was that when parents have a higher risk of running an energy deficit while foraging, offspring have a poorer chance of surviving to independence. In terms of penguins, there are a couple of studies that investigate the relationship between penguins and krill in terms of the effect of penguins on the behaviour and habitat choice of krill and the resulting effects on the foraging behaviour of penguins (Alonzo et al., 2003a; Alonzo et al., 2003b). Although based in the breeding season when the penguin is confined to a central foraging place, these studies do not consider the provisioning of a chick nor the result in terms of foraging trips and energy levels. The current model is therefore a unique way of applying a dynamic state variable model to examine the provisioning behaviour of an animal constrained to a central foraging place, taking into account variability in conditions and increasing demands of the chick.

AIM

The aim of this chapter is to create a dynamic state variable model to examine the foraging behaviour of a typical female macaroni penguin during the guard stage at South Georgia. The female responds to variable conditions in terms of krill availability, time of day and increasing demands of the chick. The model predicts the foraging effort of the female over the guard stage in terms of foraging trip duration and range. Fitness

is measured in terms of the energy state (in terms of stomach fullness) of the female and chick over time.

METHODS

The penguin behaviour model

The model presented in this chapter is a dynamic state variable model, where the mother penguin (hereafter referred to as the female) makes simple behavioural decisions at each time step based on state parameters to maximise fitness. The state of the penguin is considered in terms of stomach fullness of the female and the chick, and distance from nest. The female can choose to swim further out to sea, to swim back towards the nest, to forage, or to feed the chick. Predictions of the model are given as the distance of the female from the nest during excursions, food allocated to the female, and food allocated to the chick throughout the guard stage. The main forcing function is the availability of krill, as prey for the penguin, with increasing distance from the nest. Sensitivity analyses examine how the penguin responds to different types of distribution and availability of krill.

A number of parameters were required for the model, and these are justified below (Table 2.1).

Parameters

Table 2.1. List of parameters used in the model.

Symbol	Parameter	Value	Unit
$F(f,d,ch,t)$	Fitness increases when chick is fed, decreases with fitness costs c_p and c_{ch}	-	-
$F(T)$	Terminal fitness reward	-	-
β	Risk of mortality	0	-
i	Behavioural decisions made by female at each time step	1 to 4	-
n	Number of individuals in the forward iteration	1000	-
t	Time step	1	h
T	Final time	552	h
L	Time of day	1 day or 2 night	-
d	Distance from nest	0 to d_{max}	km
d_{max}	Maximum distance	70	km
Δd	Distance travelled per hour (speed)	5	km h ⁻¹
f	Krill in female's stomach	0 to f_{max}	g
f_{max}	Maximum stomach contents	2400	g
f_{day}	Krill required to meet daily energy demands	1200	g
Δf	Digestion of krill per hour, from stomach	$f_{day} / 24 = 50$	g h ⁻¹
hf	Time with an empty stomach, for the female	0 to 48	h
c_f	Cost of female going for one hour on an empty stomach	0 to 2	-
Y	Krill eaten after 1 hour foraging	Depends on $K(d,t)$	g h ⁻¹
ch	Krill in stomach of chick	0 to ch_{max}	g
ch_{max}	Maximum capacity of chick's stomach, increases daily	0 to 350	g
ch_{day}	Krill required to meet chick's daily energy demands, increases each day	0 to 350	g
Δch	Digestion from chick stomach per hour, linearly related to ch_{max}	$ch_{day} / 24 = 0$ to 14.6	g h ⁻¹
hc	Time with an empty stomach, for the chick	0 to 48	h
c_{ch}	Cost of chick going for one hour on an empty stomach	0 to 2	-
X	Food fed to chick	0 to ch_{max}	g
$K(d,t)$	Krill ingested after 1 hour foraging at distance d , time t	0 to f_{max}	g h ⁻¹

The fitness function F relates linearly to the amount of food fed to the chick. Even though the parent has another opportunity to breed the following year, the survival of the chick is crucial, as parents produce only one chick per year (Williams, 1980; Williams, 1989). Investment from both parents is, therefore, high and can also affect their condition for the following breeding year (Barlow and Croxall, 2002a). Therefore, in the model, there is a cost to fitness when the female or chick has an empty stomach, representing a decrease in both the probable survival of the present chick and future breeding success.

The fitness reward at the final time $F(T)$ is based simply on the actions of the female penguin at the final time step. At this time, there is one final opportunity to feed the chick, adding to fitness, and a final opportunity for a cost to fitness based on stomach fullness levels of both the female and the chick.

The risk of mortality β is zero for the female and chick in the model. The only potential threat to foraging macaroni penguins at Bird Island during January is from leopard seals, and potentially Antarctic fur seals, but in most areas they have little effect on penguin foraging behaviour (Jansen et al., 1998).

The female can adopt one of 4 behavioural decisions i at each time step, choosing the one that will optimise fitness based on the state parameters f , ch and d (Table 2.1). At sea, the female chooses from one of three decisions: to swim away from the nest, to swim back to the nest, or to forage at the current distance. At the nest, the female chooses either to feed the chick or to swim away from the nest. The behavioural decision made affects the value of some or all of the state variables.

Given that the approximate length of the guard stage is 23 days (Barlow and Croxall, 2002a; Williams and Croxall, 1991) and that the average length of foraging trips is around 16 hours (Barlow and Croxall, 2002b), it is reasonable to adopt a one hour decision interval in the model. Therefore, the final time in the model T is 552 hours, equal to 23 days.

Time of day L affects the availability of krill to the penguin and is based on 16 hours of daylight and 8 hours of night, equivalent to the sidereal cycle at South Georgia in January.

The female's location during a foraging trip is expressed as a 1-D distance from nest d . This represents a simple trade-off between the decision to travel further from the nest to gain a potentially larger reward versus a shorter trip for less reward. Direction was not included in the model because it would not add much to this principal trade off, which is a crucial one during the guard stage when the female is under high pressure to return regularly to feed the chick and is thus very constrained to the island (Barlow and Croxall, 2002b). In addition, there is little evidence for whether Antarctic fur seals and macaroni penguins choose their direction based on where they last fed successfully, the direction other predators are travelling, or in relation to physical factors such as currents or temperature gradients (Hunt et al., 1992).

The minimum distance is when the female is at the nest. Maximum distance, d_{\max} , is 100 km, representing 20 hours of travelling at 5 km h^{-1} . Estimates of travelling speed in the field come from satellite tracking data, using distance and time between data points

(Barlow and Croxall, 2002b). This method gives a lower estimation of swimming speed for macaroni penguins, at 4 km h^{-1} (Barlow and Croxall, 2002b) compared to other methods, for example experiments in swimming pools, where studies estimate 7.5 km h^{-1} on average, ranging from 7.0 to 8.2 km h^{-1} (Brown, 1987b; Clarke and Bemis, 1979). Kerry *et al.* (1995) also found lower travelling speeds using satellite positioning, compared to other techniques. An estimate of 5 km h^{-1} was used for the model, which is realistic because during the one-hour time step, the female may be searching for food or not travelling in a straight line. In addition, this gives a maximum distance of 100 km from the nest from 20 hours of travelling one way, which is sufficient, given that Barlow (2002b) estimated most trips during chick rearing to be within 50 to 60 km from Bird Island for a round trip of 16 hours on average.

The stomach fullness of the female f is measured in grams of krill. During the breeding season, macaroni penguins feed almost exclusively on krill. In some years the stomach contents of the foraging parents have no less than 90% krill (Croxall *et al.*, 1993). During chick rearing, a 3.8 kg female requires 3973 kJ day^{-1} (Davis *et al.*, 1989). Krill energy content is 4.6 kJ g^{-1} (Clarke, 1984), and assimilation efficiency of macaroni penguin adults is around 75% (Cooper, 1977; Davis *et al.*, 1989), so the female has a daily requirement f_{day} of $1200 \text{ g krill day}^{-1}$, as estimated by Croxall (1993).

I assumed that the stomach, at its maximum capacity, f_{max} , could hold 2400 g , twice the female's daily requirement of krill. Although the total capacity of the stomach is unknown, Williams (1982) recorded maximum meal sizes of chicks to be as large as 1.2 kg , which suggests that the female can hold more than her own requirement of krill for the day.

Digestion of krill per hour Δf signifies the amount of krill required to meet the energetic requirements described above. The female needs 1200 g krill per day to meet her energy requirements (Boyd, 2002a; Croxall et al., 1993), so every hour, 50 g krill, Δf , is subtracted from the stomach contents. The penguins in the model use an equal amount of energy throughout the day, although the actual metabolic rate of macaroni penguins at sea is potentially greater than their metabolic rate on land, with Green *et al.* (2002) estimating $\sim 9.0 \text{ W kg}^{-1}$ and $\sim 6.3 \text{ W kg}^{-1}$ respectively.

The parameter hf indicates the time that the female has endured an empty stomach. This measure translates directly into the fitness cost, c_f , for each hour without food. The fitness cost and hf ranges from 0, the female has food in her stomach, to -48 , the female's stomach has been empty for 48 hours. The cost to fitness does not increase further after 2 days on an empty stomach. It is reasonable to assume a cost to fitness with failure to meet energy demands because this is likely to result in a loss of weight, therefore a loss of condition. There is evidence that female macaroni penguins lose on average 14% of their body weight during this challenging time of the guard stage (Barlow and Croxall, 2002a). In addition, the father is not receiving any of his daily energetic requirement and loses around 25% of his body weight during this time (Barlow and Croxall, 2002a).

The female at sea can increase the amount of krill in her stomach at any time by choosing to forage for one time step at her current distance from the nest. The reward from foraging Y , in grams of krill, varies according to the krill availability function $K(d, t)$. This parameter describes krill availability with distance from nest and time of day,

representing how much krill the female ingests after one hour of foraging. If krill availability is high, then Y is truncated so that the stomach is only ever filled to its maximum capacity f_{\max} .

The macaroni penguin chick has increasing daily energy demands as it grows; measured in this model by the amount of krill it requires each day, ch_{day} . Estimates of maintenance and energetic requirements of macaroni chicks range from 420 kJ d⁻¹ in the first week, to 770 kJ d⁻¹ in the second week, and 1250 kJ d⁻¹ in the third week from hatching (Brown, 1987a). An assimilation rate of 0.75 gives a daily requirement of $1250/0.75 = 1666$ kJ d⁻¹ as the chick reaches the end of the guard stage (Cooper, 1977). Further, taking into the account the energy content of krill, at 4.6 kJ g⁻¹ (Clarke, 1984), chicks require an average of $1666/4.6 = 362$ g krill d⁻¹ at this age. Croxall *et al.* (1993) calculated a similar figure for chick energy requirements of 350 g krill d⁻¹ around this time of year. Although it is possible that chick energy demands do not increase linearly (Brown, 1987a)(Figure 2.1), there is little quantitative evidence for the relationship. In addition, chick growth in mass up until 23 days of age is approximately linear (Barlow and Croxall, 2002a; Brown, 1987a). Considering these factors, a linear parameterisation of chick energy requirements in the model was considered appropriate.

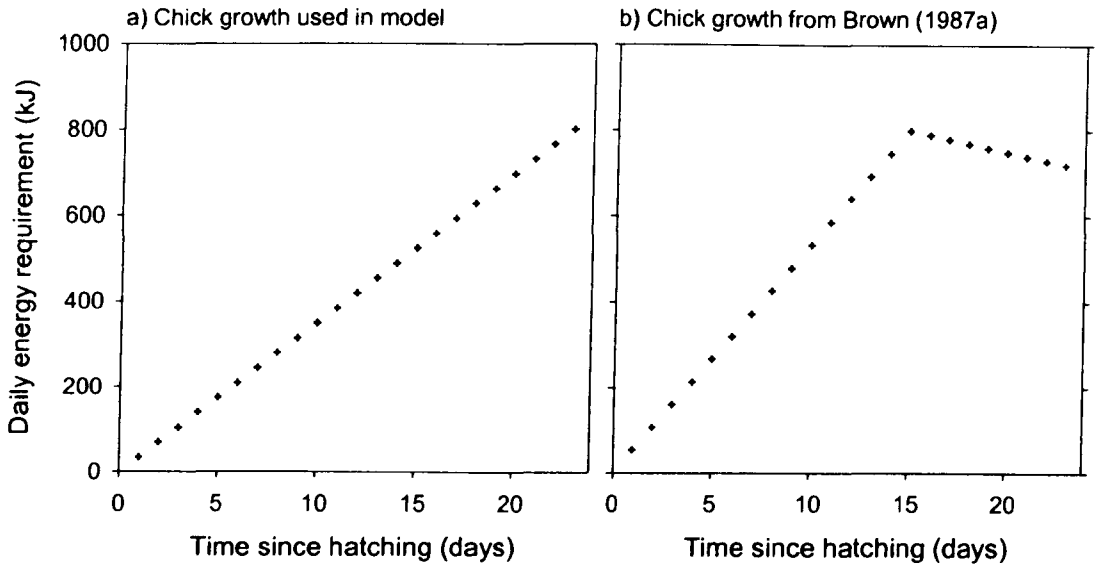


Figure 2.1. Chick energy requirements in kJ d^{-1} for a) energy requirements in the model and b) energy requirement estimated by Brown (1987a).

The maximum stomach capacity of the chick, ch_{\max} , at any time is equal to the krill requirement for that day, ch_{day} . Williams (1982) noted that, in the first 10 days after hatching, recently fed penguin chicks had extremely swollen abdomens. He concluded that the female, in order to reduce foraging time and effort, probably fed as large a quantity to the chick as possible and that the chick probably ate as much food as it could contain. It is unknown exactly how much food an individual chick can contain, however the daily energetic requirement is considered a reasonable estimate.

The digestion of krill from the chick's stomach, Δch , like the female, represents a usage of energy throughout the day. In addition, for the chick, energy usage Δch increases daily as the energy requirement of the chick increases, but remains constant each hour of the day. For example, a chick that is 20 days old requires ~ 305 g krill to meet energy demands for that day, so it digests $305/24 = 12.7$ g krill per hour throughout day 20. Like the female, if the chick's stomach is empty for a time there is a corresponding

fitness cost. This is recorded by the parameter hc . The fitness cost for the chick going an hour c_{ch} on an empty stomach is equal in magnitude to the fitness benefit when the mother feeds the chick the krill requirement for one hour. It is reasonable to assume this relationship, considering that the average growth rate of frequently fed chicks is $\sim 63 \text{ g d}^{-1}$ (Croxall et al., 1993) is approximately equal in magnitude to the average mass decrease of unfed chicks recorded at $\sim 65 \text{ g d}^{-1}$ (Williams and Croxall, 1991).

The availability of krill $K(d,t)$ has a positive linear relationship with distance from nest in the model (Figure 2.2). There is some evidence that the concentration of krill increases toward the shelf edge, and areas of turbulence (Makarov et al., 1988; Witek et al., 1981), but decreases past this region off the shelf (Trathan et al., 2003). During the guard stage, macaroni penguins forage mainly over the shelf and shelf break (Barlow and Croxall, 2002a), so it is not necessary to consider the decrease in krill abundance past this region. In addition, there is more competition for food inshore when many predators forage from a small island, which may decrease the availability of krill close to shore.

Krill availability also varies over the course of the day, which is important to macaroni penguins given that they are visual predators and tend to dive predominantly in daylight (Green et al., 2003). However, it is possible that they do have some success at night (Croxall et al., 1993), with Green *et al.* (2003) reporting dives at night to be less frequent, shallower and shorter than dives during the day. In addition, although visibility is reduced at night, the krill resource is likely to be more dispersed and shallow due to a diel vertical migration (DVM) for minimising predation and maximising food intake (De Robertis, 2002; Eiane and Parisi, 2001; Godlewska, 1996;

Hays, 2003; Ritz, 1994). However, there is no quantitative data on macaroni penguin foraging success with time of day. In the model, krill availability at night is ten times less than during the day for each distance (Figure 2.2).

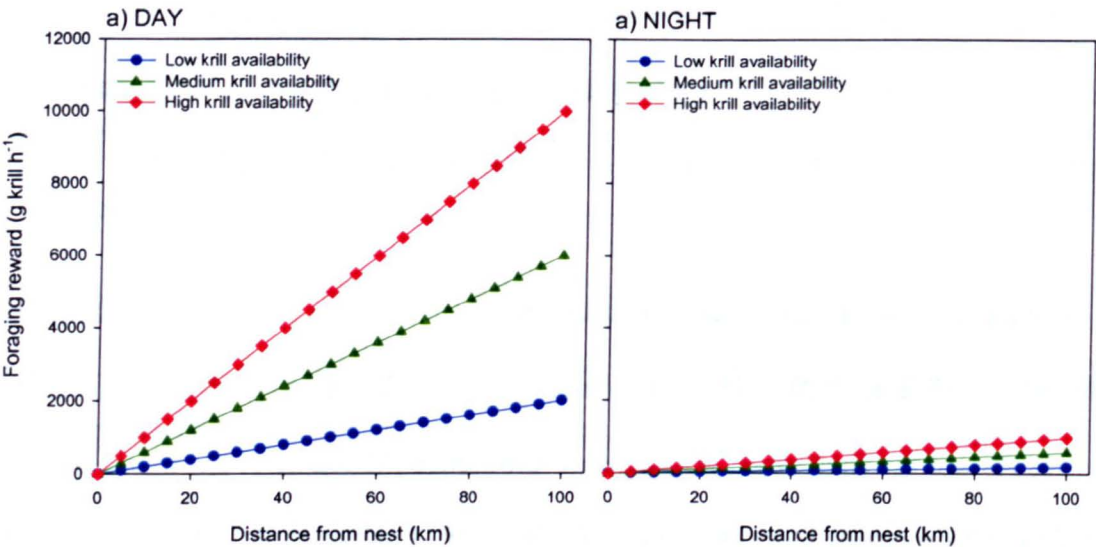


Figure 2.2. Foraging reward with distance from nest in years of low, medium and high krill availability, representing the krill intake from one hour of foraging at the specified distance. The foraging reward (Y) increases linearly with distance from nest (d) such that $Y= dka$, where $k=$ g of krill eaten per hour, $a = 20, 60$ or 100 in the day and $2, 6$ and 10 at night for low, medium and high krill availabilities respectively.

The inclusion of stochasticity in the model is a way to represent patchiness in the krill resource. Krill are highly variable in space and time due to their swarming behaviour and diel vertical migration (Godlewska, 1996; Marr, 1962). In addition, krill are variable in terms of distribution on the landscape, both because they can be transported long distances by currents and because they feed on phytoplankton that is patchy in space and time (Atkinson et al., 2001; Fach et al., 2002; Hofmann and Murphy, 2004). The following four scenarios describe different types of krill variability.

The first $K(d,t)$ is a scenario where the mean reward of krill per hour foraging does not change with distance, but the normal standard deviation around the mean decreases linearly with increasing distance from nest. This represents a situation where the reward for foraging one hour close to shore may result in the location of a swarm, in which case the reward is high, or failure to locate a swarm, with a resulting low reward. There is some evidence that krill may form denser swarms on shelf where predation is high, and more dispersed swarms further out to sea where predation is low. Some authors suggest that, once located, a dense swarm is more rewarding because of a high concentration of krill (Hofmann et al., 2004). However, in a dense swarm, krill have increased vigilance and group avoidance strategies that have probably evolved in response to visual predators such as penguins (Obrien, 1987; Ritz, 2000). In addition, denser swarms of krill mean a more patchy resource, which also makes them harder to locate. In the model, variability is proportional to the mean for years of low, medium and high krill availability (Figure 2.3).

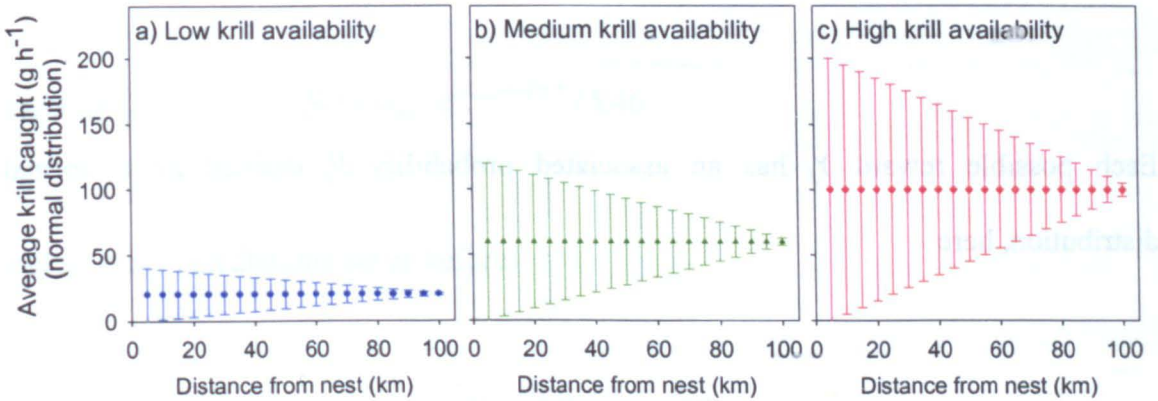


Figure 2.3. The mean availability of krill per hour: constant with distance from nest but different for years of low, medium and high krill availability. The bars represent the maximum range of rewards around the mean for a normal distribution, with maximum range and corresponding standard deviation decreasing linearly with increasing distance from nest.

In this first scenario, the standard deviation SD around the mean μ is calculated

Equation 2-1
$$SD = \frac{\mu_{\text{int}} \cdot [(d_{\text{max}} + 1) - d]}{2}$$

where μ_{int} gives the interval of possible rewards in relation to the mean, if the mean is varied for each simulation, such that

Equation 2-2
$$\mu_{\text{int}} = \mu / 10$$

There are $j = 0$ to 21 possible foraging rewards, Y_j , at each distance, equally spaced about the mean, such that

Equation 2-3
$$Y_j = \mu_{\text{int}} \cdot j$$

Each possible reward Y_j has an associated probability P_j defined by a normal distribution, here

Equation 2-4
$$P_j = \exp\left(-\frac{(Y_j - \mu)^2}{2 \cdot SD^2}\right)$$

Variability type II

The second parameterisation of $K(d,t)$ is similar to the first, where the mean krill reward does not change with distance but, in this case, the standard distribution around the mean decreases exponentially with increasing distance from nest (Figure 2.4).

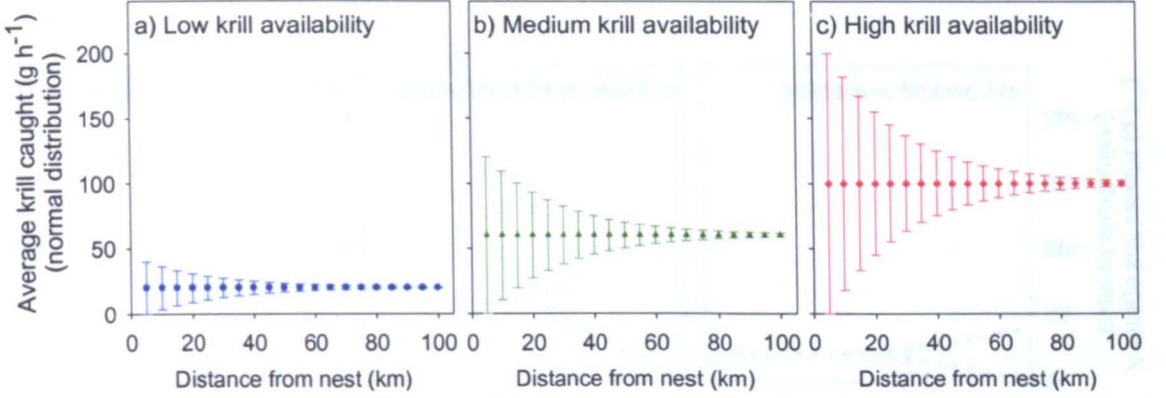


Figure 2.4. The mean availability of krill per hour: constant with distance from nest but different for years of low, medium and high krill availability. The bars represent the maximum range of rewards around the mean for a normal distribution, with maximum range and corresponding standard deviation decreasing exponentially with increasing distance from nest.

In this parameterisation, the standard deviation SD around the mean μ is calculated

Equation 2-5
$$SD = \mu_{\text{int}} \cdot e^{(d_{\text{mas}} + 1 - d)/5} / 5.46$$

and all other calculations are as before.

Variability type III

The third parameterisation of $K(d,t)$ is similar to the first, where the mean krill reward does not change with distance, but instead of a normal distribution around the mean, there is a binomial distribution. As distance increases, the possible rewards become closer to the mean until after distance 50 km, the only possible reward is the mean krill

availability tested (Figure 2.5). This represents a situation, like the first tested, where the penguin may forage for an hour close to the nest and either find a large swarm, in which case the reward is high, or not find a swarm at all. Further from the nest, the krill resource is likely to be less dispersed, and so the penguin is more likely to find the mean reward of krill after one hour foraging.

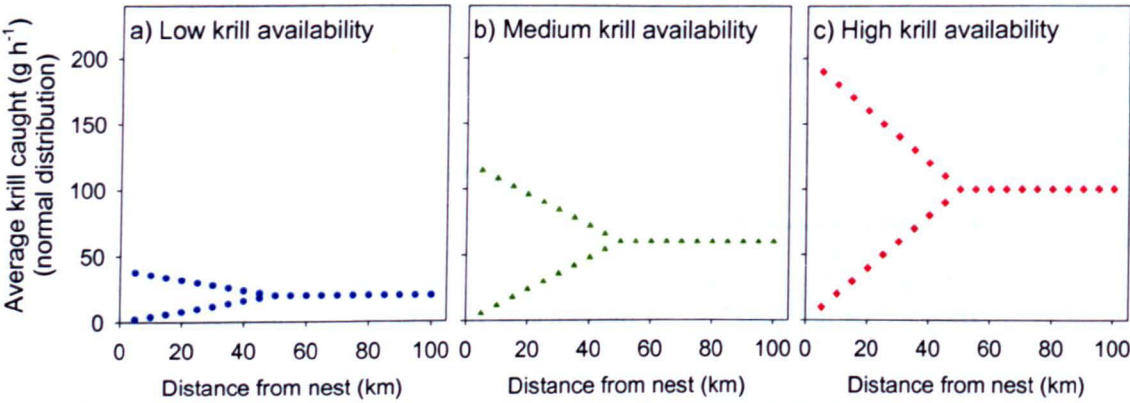


Figure 2.5. Below 50 km from nest there is a binomial distribution of krill, with only two possible outcomes of equal probability at each distance from nest. Each value is the mean krill availability \pm a factor that decreases linearly with distance. From 50 to 100 km from nest, there is only one possible reward for foraging one hour, equal to the mean availability of krill for each of the scenarios.

For distance $d \leq 50$, there are $j = 1$ to 2 possible foraging rewards, Y_j , at each distance, equally spaced above and below the mean, such that

Equation 2-6
$$Y_j = \mu + (-1)^j \cdot \frac{(10-d)}{10} \cdot \mu$$

Each possible reward Y_j has an associated probability P_j , here

Equation 2-7 $P_j = 0.5$

When distance $d > 50$, there is only $j = 1$ possible reward at each distance from the nest, equal to the mean availability of krill for each simulation.

Equation 2-8 $Y_j = \mu$

with a corresponding probability

Equation 2-9 $P_j = 1$

Variability type IV

The final scenario is different, where both krill availability and variability increase with increasing distance from the nest (Figure 2.6). This represents a situation where the penguin is likely to have a low reward from foraging close to the nest, but likely to have a higher but also more variable reward further away. This is a combination of the fact that although krill concentration may be higher on shelf than off shelf (Hunt et al., 1992; Makarov et al., 1988; Witek et al., 1981), inter- and intra-specific competition, combined with higher density of krill swarms, means that krill availability is low. In addition, there is some evidence that krill concentration is higher at the shelf break (Trathan et al., 2003).

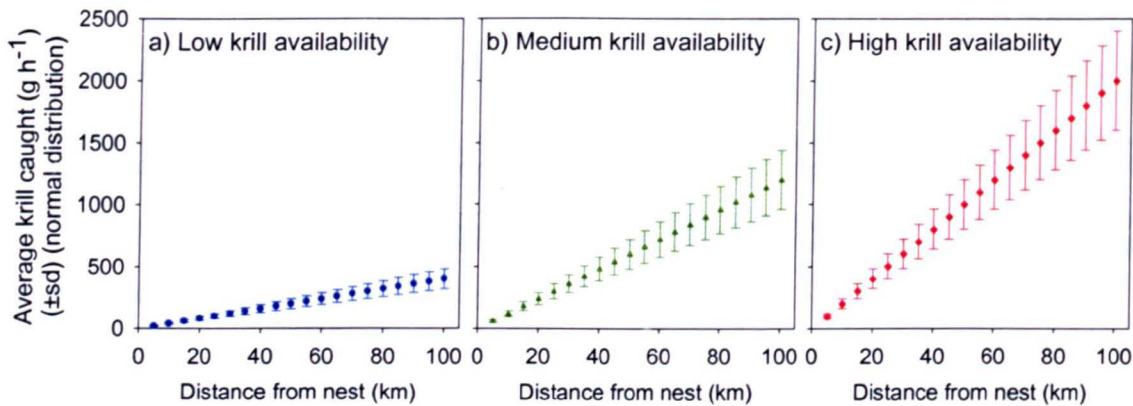


Figure 2.6. Both the mean availability and variability of krill increases with increasing distance from nest. The mean availability of krill per hour: increases with distance from nest and is different for years of low, medium and high krill availability. The bars represent the maximum range of rewards around the mean for a normal distribution, with maximum range and corresponding standard deviation increasing linearly with increasing distance from nest (Equation 2-10).

In this parameterisation, the mean changes with distance and food level as in the best estimate parameterisation of the model (Figure 2.2), with the standard deviation SD around the mean μ calculated

Equation 2-10 $SD = \mu_{int} \cdot 2$

All other calculations are as for variability type I and II.

Running the model

The backward iteration

The following describes firstly the simplest model tested that considers only the state parameters of female stomach fullness f , distance from nest d , and time t . Further

descriptions include the addition of cumulative fitness when the chick is fed and a fitness cost for failure to meet energetic demands.

The female penguin chooses one decision each time step. When distance from the nest

$d > 0$, the female is at sea and considers decisions:

$i = 1$: swim away from the nest

$i = 2$: swim towards the nest

$i = 3$: forage at current distance

When $d = 0$, the female is at the nest and considers decisions:

$i = 4$: feed the chick

$i = 1$: travel away from the nest

Although the parameters were defined in grams of krill, these were converted into hours' worth of krill for the running of the model and the fitness calculations. Therefore, the daily requirement of the female was 24 h worth of krill, the equivalent of 1200 grams of krill. Digestion was 1 h worth of krill per time step, the equivalent of $1200/24 = 50$ grams of krill. Therefore, for the female, the return from foraging in grams of krill was divided by 50 to give the amount of krill in hours worth of the daily requirement. Likewise, for the chick, the daily requirement in grams of krill was divided by 24, giving the hourly requirement of krill. For the chick, although this value increased each day, one hour's energy requirement at 1 day old was equal in fitness terms to one hour's energy requirement at 10 days old.

The decision chosen at time t is that which maximises the fitness at time $t + 1$ calculated from resulting stomach contents state f and distance state d . The decision chosen also has a resulting effect on the state parameters at time $t + 1$ (Figure 2.7).

	t	$t + 1$	t	$t + 1$	
$i = 1$	<div> <div> <div>f_{\max}</div> <div>f</div> <div>0</div> </div> <div> <div>Δf</div> </div> </div>	<div> <div> <div>f_{\max}</div> <div>f'</div> <div>0</div> </div> </div> $f' = f - \Delta f$	<div> <div> <div>d_{\max}</div> <div>d'</div> <div>0</div> </div> </div> $d' = d + \Delta d$	<div> <div>d_{\max}</div> <div>d'</div> <div>0</div> </div>	swim out: food in gut decreases by Δf (digest 1 hour energy requirement), distance from nest increases by Δd
$i = 2$	<div> <div> <div>f_{\max}</div> <div>f</div> <div>0</div> </div> <div> <div>Δf</div> </div> </div>	<div> <div> <div>f_{\max}</div> <div>f'</div> <div>0</div> </div> </div> $f' = f - \Delta f$	<div> <div> <div>d_{\max}</div> <div>d'</div> <div>0</div> </div> </div> $d' = d - \Delta d$	<div> <div>d_{\max}</div> <div>d'</div> <div>0</div> </div>	swim back: food in gut decreases by Δf and distance from nest decreases by Δd (distance travelled in 1 hour)
$i = 3$	<div> <div>Y</div> <div> <div> <div>f_{\max}</div> <div>f</div> <div>0</div> </div> <div> <div>Δf</div> </div> </div> </div>	<div> <div> <div>f_{\max}</div> <div>f'</div> <div>0</div> </div> </div> $f' = f - \Delta f + Y$	<div> <div> <div>d_{\max}</div> <div>d'</div> <div>0</div> </div> </div> $d' = d$	<div> <div>d_{\max}</div> <div>d'</div> <div>0</div> </div>	forage: Δf is digested, then Y (food intake) added from foraging, distance does not change
$i = 4$	<div> <div> <div> <div>f_{\max}</div> <div>f</div> <div>0</div> </div> <div> <div>Δf</div> <div>X</div> </div> </div> </div>	<div> <div> <div>f_{\max}</div> <div>f'</div> <div>0</div> </div> </div> $f' = f - \Delta f - X$	<div> <div> <div>d_{\max}</div> <div>d'</div> <div>0</div> </div> </div> $d' = d = 0$	<div> <div>d_{\max}</div> <div>d'</div> <div>0</div> </div>	feed chick: Δf digested, parent feeds chick X from remaining gut contents, distance 0 (at nest)

Figure 2.7. The result of choosing one of decisions $i = 1$ to 4 at time t , giving the resulting stomach contents and distance from nest for the female at time $t + 1$.

In addition, the decision chosen has an effect on the state of the chick (Figure 2.8).

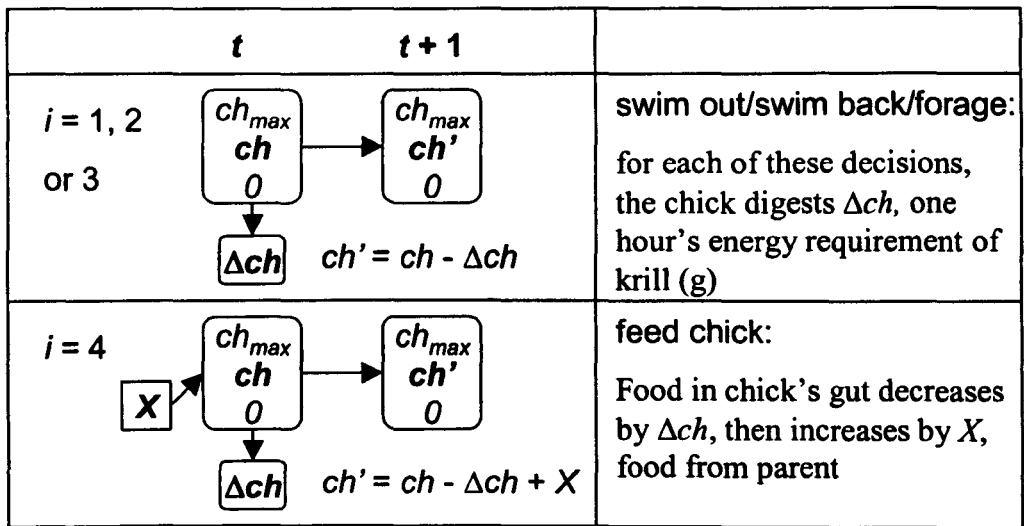


Figure 2.8. The effect of each of the decisions made by the female on the stomach contents of the chick ch , showing when the decision is made at time t to its effect at time $t + 1$.

The dynamic programming algorithm is where fitness F at time t is calculated by the female making the decision i that would maximise fitness at time $t + 1$.

Equation 2-11

$$F(f, ch, hf, hc, d, t) = \max_i [F(f'_i, ch'_i, hf'_i, hc'_i, d'_i, t + 1) + X_i - hf \cdot c_f - hc \cdot c_{ch}]$$

Y_i is the food reward resulting from decision i , and Δf is the amount of food in the female's stomach digested each hour.

Equation 2-12

$$f'_i = f - \Delta f + Y_i$$

The stomach contents state will only take values ranging from 0 to f_{max} .

Equation 2-13

$$Y_i = \begin{cases} f_{\max} - (f - \Delta f) & ; f_i' > f \\ Y_i & ; f_i' \leq f_{\max} \end{cases}$$

Likewise, distance state will only take values ranging from 0 to d_{\max} .

The parameter measuring hours on an empty stomach for the female hf increases in the next time step only if the female's stomach is empty. If there is food in the female's stomach then $hf = 0$.

Equation 2-14

$$hf_i' = \begin{cases} hf + 1 & ; f_i' = 0 \\ 0 & ; f_i' > 0 \end{cases}$$

Likewise, for the chick, hc can only increase if the chick's stomach contents are empty.

Equation 2-15

$$hc_i' = \begin{cases} hc + 1 & ; ch_i' = 0 \\ 0 & ; ch_i' > 0 \end{cases}$$

The fitness cost of having an empty stomach is multiplied by a factor for both the female and chick, c_f and c_{ch} respectively, which is 1 for the best estimate model. Different factors are tested in the sensitivity analysis.

X_i is the food fed to the chick, only when $i = 4$. This means that fitness accrues during each time period, so that the expected lifetime fitness function is now the sum of the expected per-period fitness increments and the terminal fitness function (Mangel and Clark, 1988). Δch is the food digested from the chick's stomach each time step.

Equation 2-16 $ch'_i = ch - \Delta ch + X_i$

The chick stomach contents state will only take values ranging from 0 to ch_{\max} . This affects the amount of food X_i that can be fed to the chick at any time.

Equation 2-17
$$X_i = \begin{cases} ch_{\max} - (ch - \Delta ch) & ; \quad ch'_i > ch_{\max} \\ X_i & ; \quad ch'_i \leq ch_{\max} \end{cases}$$

Adding variability

Variability in food rewards was implemented through applying the type I to IV scenarios for variability in krill availability described previously (pages 10-14). The fitness algorithm is modified for a model with variability, where j is one of 21 possible rewards.

Equation 2-18

$$F(f, ch, hf, hc, d, t) = \max_i \sum_{j=1}^{21} P_j \cdot [F(f'_{ij}, ch'_i, hf'_i, hc'_i, d'_i, t+1) + X_i - hf \cdot c_f - hc \cdot c_{ch}]$$

The forward iteration

In the forward iteration, the model was run for a model period of 552 hours, the length of the guard stage, for 1000 individuals. In the forward iteration, the female chose the behaviour each time step according to the optimal policy based on the state parameters. The model was run firstly without any variability, with best estimate parameterisation (Table 2.1). Results show the average behaviour of the female, in terms of foraging trip distance, duration and rest between trips, and the average energy level of both the

female and chick. Next, variability was added to the model, with all parameters except for krill availability at best estimate predictions. For krill availability, the values for foraging reward were randomly sampled from a probability distribution that differed for each type of variability tested (for example, Equation 2-4). This means that if the values for foraging reward were randomly generated 1000 times, the distribution of rewards would correspond to the probability distribution of the variability type (I to IV).

Finally, sensitivity analyses were performed on the model by changing specific variables one at a time while keeping best estimate parameterisation for the rest of the model. These changes are detailed in Table 2.2.

The sensitivity analysis

To test the robustness of the model, a number of parameters were varied through a range of values (Table 2.2).

Table 2.2. List of parameters tested in the sensitivity analysis. Values in bold are those used in the best estimate parameterisation.

Symbol	Parameter	Values tested	Unit
$K(d,t)$	Krill ingested after 1 hour	5 different functions in total, described	grams
	foraging at distance d, time t	in the text above	krill h ⁻¹
d_{max}	Maximum distance	50, 100 , 150, 200	km
f_{max}	Maximum stomach contents of the female	600, 1200, 1800, 2400 , 3000, 3600	grams krill
ch_{max}	Maximum capacity of chick's stomach, changes each day	ch_{day} * 1 , ch _{day} * 2, ch _{day} * 3, ch _{day} * 4	grams krill
(c_p, c_{ch})	Cost to fitness for female and chick having an empty stomach	(0,0) (0,1) (1,1) (2,1) (2,2)	-

Krill as a resource are variable in space and time (Godlewska, 1996; Hofmann and Murphy, 2004; Marr, 1962; Murphy et al., 1998). However, it is not clear exactly how this affects their availability to predators on a small scale. A number of scenarios were tested for the availability of krill with increasing distance from nest, and these are described in the previous section. The maximum distance from nest was varied, because, while macaroni penguins are believed to stay within 50 to 60 km of the nest during the guard stage (Barlow and Croxall, 2002b), it is possible they may travel further. Changing this parameter could also give some indication of whether the travelling speed was accurately estimated in the model. The maximum stomach capacity of both the female and chick were varied. The maximum stomach capacity of the female affects the maximum amount of krill she can consume at any time, therefore affecting the size of the meal delivered to the chick. While the approximate daily requirement of krill has been estimated in the field (Croxall et al., 1993), the maximum stomach capacity of female macaroni penguins is unknown. The stomach capacity of the chick is also an important parameter to test because it affects how often the female has to return to feed the chick. If the chick has a large stomach capacity then it becomes possible for the female to feed the chick more than one day's requirement at one feeding. In the field, the maximum stomach capacity of macaroni penguin chicks is unknown.

Finally, it was necessary to test a number of scenarios for the parameter specifying fitness cost. While there is some understanding that the parent must consider both their own condition and the condition of the offspring in order to maximise both current and future reproductive success, it is unknown exactly how the parent balances this decision in terms of maximising fitness. In addition, given the unique approach used in this

model, it is important to test this parameter thoroughly. Williams and Croxall (1991) demonstrated that unfed macaroni penguin chicks decreased by an amount of weight each day that was equivalent to the weight increase of a regularly fed chick (Croxall et al., 1993). In addition, the female macaroni penguin loses on average 14% of her body weight over the guard stage, with the male losing 25% (Barlow and Croxall, 2002a). This suggests that a failure to meet energy demands results in a loss of weight, which is effectively a loss of body condition, having potentially both immediate and future negative effects on breeding success and therefore fitness. The values tested ranged from (0,0) no cost for either female or chick, to (2,2) a fitness cost of 2 for both female and chick, where the number to the left specifies the cost for the chick, and the number on the right the cost for the female (Table 2.3).

Table 2.3. Explanation of the numbers representing the cost to fitness for the female or chick going on an empty stomach.

Fitness cost	Explanation
0	No cost for having an empty stomach
1	The fitness cost for 1 h without food is equal to the benefit of being fed 1 h energy requirement
2	The fitness cost for 1 h without food is equal to the benefit of being fed 2 h energy requirement

RESULTS

The first section of results gives the predictions from a simple model where the krill reward at each distance from the nest is deterministic and not variable. The second section presents the predictions of penguin energetic and behavioural response to variability in krill, for four different scenarios of krill variability. The final section tests

the robustness of these predictions by running a number of parameters in the best estimate model through a range of values and testing the response of the model.

Best estimate results

The following graphs show the cumulative amount of krill allocated to the chick and the female as a way of representing chick growth rate and parental energy requirements. With the best estimate parameterisation of the model, the growth rate of the chick was noticeably different for model simulations with low compared to medium and high krill availability (Figure 2.9). For medium and high availability of krill, the chick received around the ideal amount of food whereas, for low krill availability, the chick did not receive any food after the initial feeding until after day 15. Although the energy limits of the chick were not parameterised in the model, this behaviour would almost certainly result in chick death.

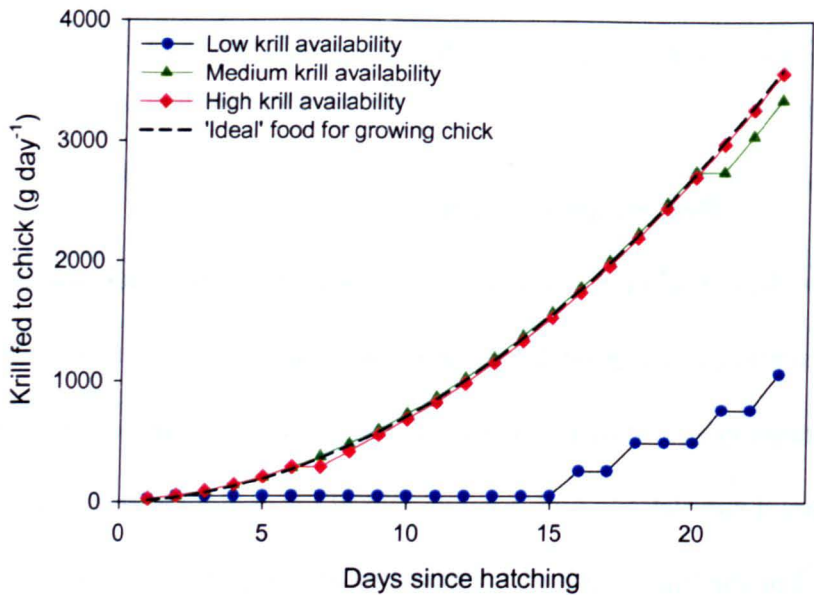


Figure 2.9. The predicted additive amount of food fed to the chick over 23 days of the guard stage, from hatching, for simulations with low, medium and high krill availability. The amount of food fed to the chick is compared with the ‘ideal’ amount needed for healthy chick growth, estimated from energetic requirements in past studies (Brown, 1987a).

The female received close to her ideal amount of food, based on energetic requirements at this time, only when krill availability was high (Figure 2.10). For low and medium krill availability, the female reduced her requirement by 15%.

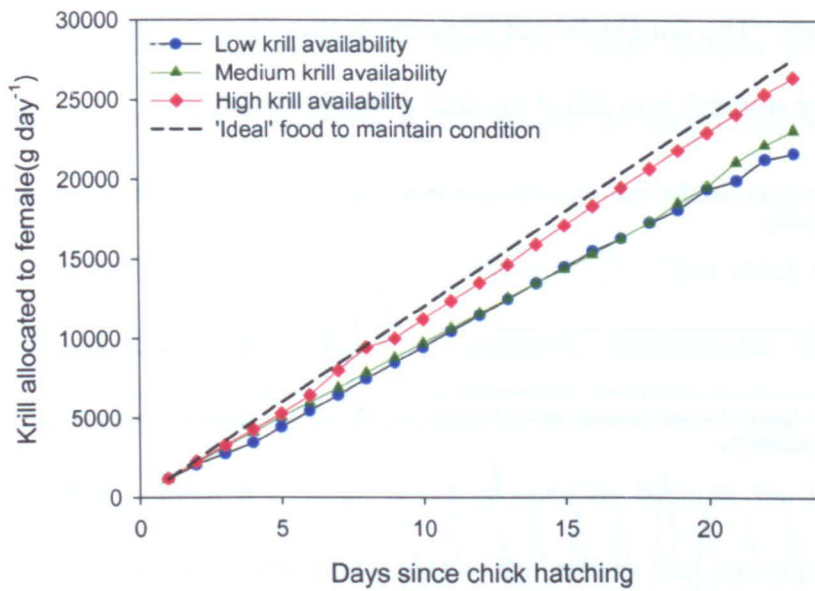


Figure 2.10. Amount of krill (g) eaten by the female minus the amount fed to the chick each day of the guard stage from hatching. 'Ideal' daily amount of krill based on energetic requirements of female macaroni penguins during the guard stage (Boyd, 2002a; Croxall et al., 1993).

Figure 2.11 graph represents the distance of the female from the nest over the 23 days of the guard stage for low, medium and high krill availability. Distance zero means the female is at the nest, so each return to zero represents a complete foraging trip. As krill availability increased, the foraging trips of the female became more frequent and further from the nest. With low krill availability, the female only made five return trips to the nest, to around 20km away. In addition, one of these foraging trips lasted around half the guard stage. The reason for the female foraging a long time close to shore is probably that the krill reward was so small for low krill availability, even further from shore, that all of the krill would have been digested by the time she returned to the chick. The only way to return with a meal was to forage further from the nest for a long time to build up enough food so that it would not be digested on the way back to the chick. With medium and high krill availability, foraging trips are around 25 hours in

general, with the female heading to 25 and 45 km from the nest for medium and high krill availability respectively. The female did not leave the nest until approximately one day had passed because her stomach was full at the start of each simulation.

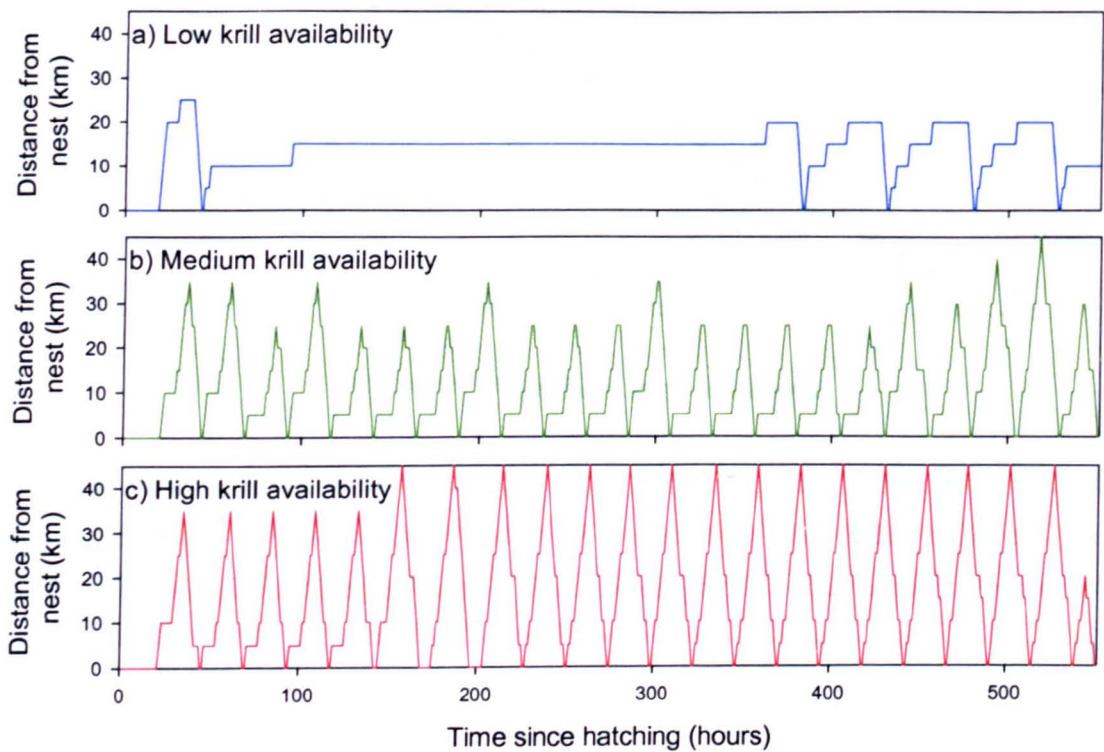


Figure 2.11. The female’s distance from the nest over time, with each return to the nest (distance 0) representing a foraging trip. Results show simulations with low, medium and high krill availability.

With variability

The following four sections give the resulting penguin growth and behaviour in response to the three different types of variability tested. Each section includes the energetic response of the chick and the female and foraging trips of the female over time to different types of krill variability.

Variability type I

The first type of variability is where the mean amount of krill is the same at each distance, but the standard deviation around the mean decreases linearly with distance from the nest. With this type of variability, the chick did not receive any food at all when krill availability was low (Figure 2.12). The chick received around the ideal amount of krill according to its energetic requirements for both medium and high availability of krill. The chick actually received more food when krill availability was medium compared to high, which is possibly because the female was sacrificing her own condition by foraging closer to the nest so that she was able to return more often with food for the chick. The female ate the ideal amount of krill only with high krill availability. For medium krill availability, she received around 10% less than her energetic requirement, and for low krill availability, she received less than half her requirement. There was more variability in the food delivered to the chick compared to that allocated to the female.

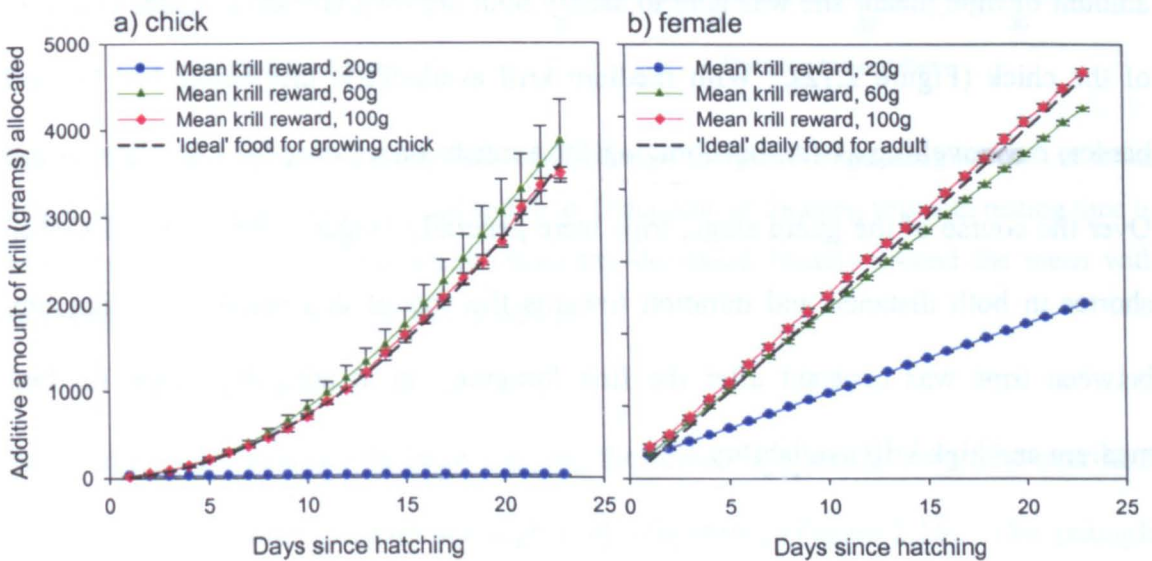


Figure 2.12. Amount of krill allocated by the female to a) the chick and b) herself over the guard stage over low, medium and high food simulations for variability type I.

The foraging trips of the female differed markedly in both distance and duration for different levels of krill availability (Figure 2.13). With low krill availability, the female made only one return foraging trip of around 22 h duration, but was at sea the rest of the guard stage, as no further resting time was recorded. The reason the female did not return to the nest is most likely that the small amount of krill she acquired would have been completely digested by the time she returned to the nest, meaning she was unable to feed the chick. As krill availability increased, the foraging trips of the female became more frequent and further from the nest. For medium krill availability, trips were to a distance of around 5 km and duration of 19 to 20 hours on average, with little variation in the maximum distance of trips but more variation in the duration between penguins. With high krill availability, foraging trips were to a greater distance, around 15 to 20 km, and shorter duration, around 15 h, than with medium krill availability. This means that with high krill availability, the female could travel further for a much higher reward, which meant less time foraging. In addition, obtaining a large meal in a shorter amount of time meant she was able to satisfy both her own energy demands and those of the chick (Figure 2.12). With medium krill availability, the female had to work harder: not travelling as far, but foraging for a much longer time for a smaller reward. Over the course of the guard stage, trips were generally longer at the start and slightly shorter in both distance and duration towards the end of this period. Resting time between trips was constant after the first foraging trip at around 2 hours for both medium and high krill availability.

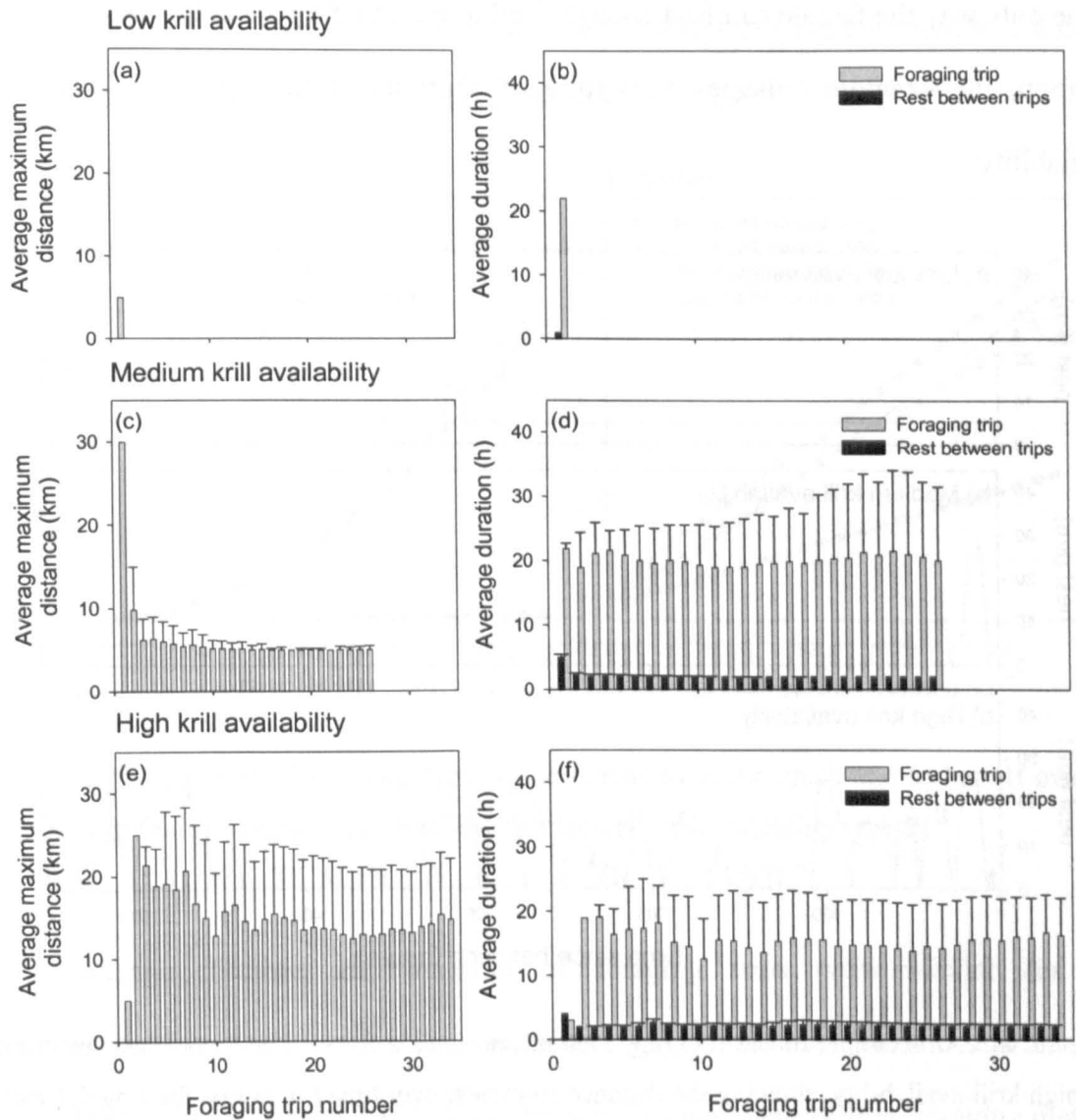


Figure 2.13. The average result for 1000 simulations of the guard stage foraging trips in terms of (a, c, e) maximum distance travelled and (b, d, f) duration of foraging trip with resting time in between (+SD), for simulations where variability decreased linearly around the mean with increasing distance from nest (variability type I).

Example trips are also shown below, giving the female's distance from nest over time for simulations of low, medium and high krill availability (Figure 2.14). The example shows that the female does not return to the nest after the initial foraging trip when krill availability is low, but remains at a close distance to the nest for the remainder of the guard stage. Most likely, the small possibility of finding a large reward close to the nest

is the only way the female can find enough food to return with a meal for the chick. In addition, the example indicates a mixture of short and long trips with high krill availability.

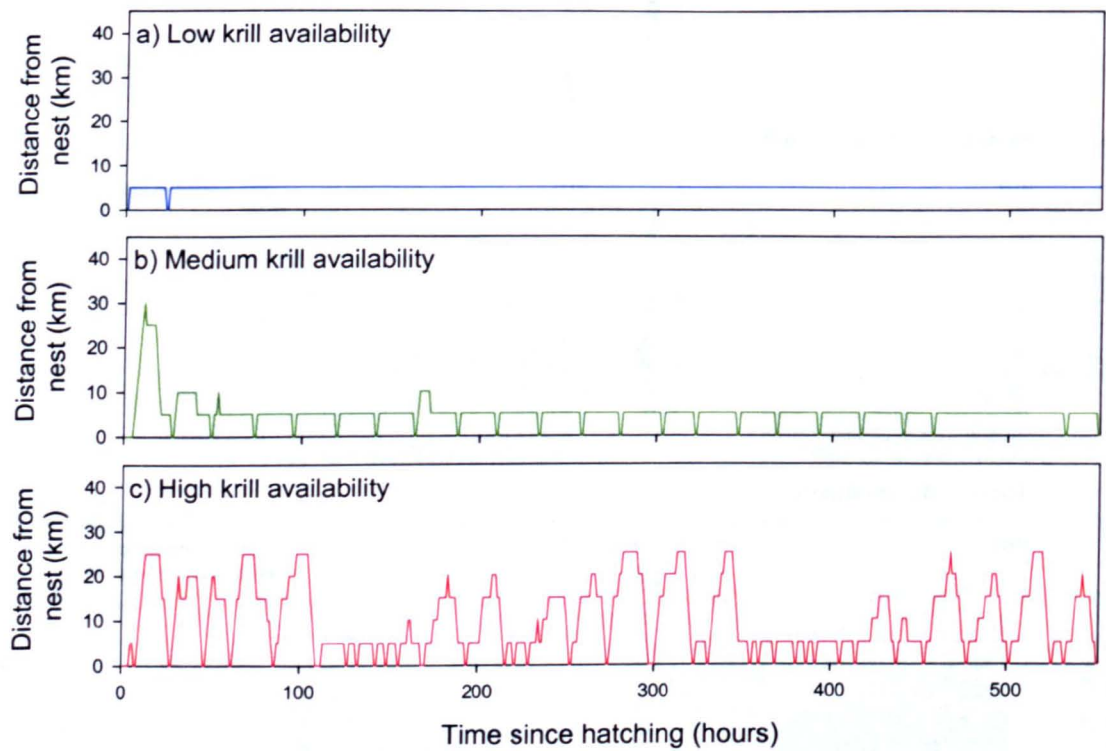


Figure 2.14. An example of the foraging trips of one female for simulations of low, medium and high krill availability, showing the distance from nest over time t in hours, for a model with variability type I.

Variability type II

In variability type II, where the mean reward of krill was the same for each distance, but this time the standard deviation decreased exponentially, the energy allocated to the chick for this type of variability (Figure 2.15) was the same as that described in the previous section (Figure 2.12). However, the results for the parent were slightly different, with the female receiving more than her energetic requirement with high krill availability, around the ideal amount for medium availability, and less than half for low

krill availability. As with variability type I, the amount of food allocated to the chick and the female was most variable with medium krill availability.

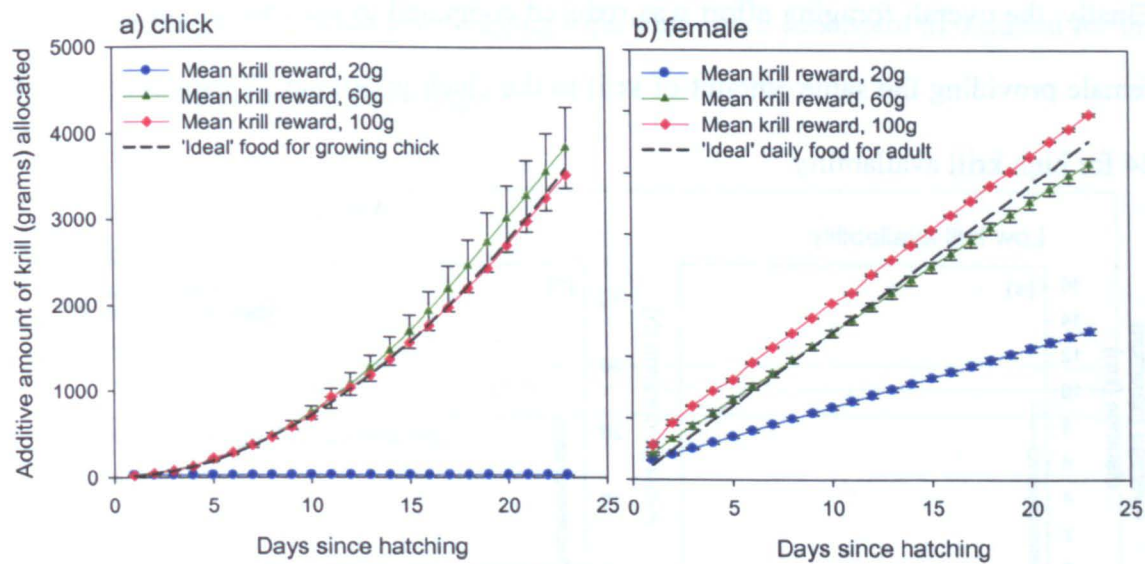


Figure 2.15. Amount of krill allocated by the female to a) the chick and b) herself over the guard stage for low, medium and high krill availability, with variability type II.

The average distance and duration of foraging trips were similar for this parameterisation compared to the variability type I scenario for low and medium availability of krill (Figure 2.16). Like the previous parameterisation, foraging distance increased and duration decreased with increasing availability of food, with trips around 17 to 23 h for medium krill availability and 14 to 20 h for high availability. In addition, when krill availability was medium, the female foraged to a further distance at the start of the guard stage compared to the end. With low krill availability, there was again only a single return foraging trip to feed the chick. However, with high krill availability, foraging trips consistently reached a maximum distance of 10 km, with a couple of trips to 15 km. Although the distance of foraging trips was relatively consistent for high krill availability, the duration of trips varied between short trips and long trips, and each individual penguin appeared to have the same strategy with no variability around the mean. For medium krill availability, the variation in foraging trip

duration between penguins increased over time. This is because, as time progresses, the female was foraging closer to the nest where krill availability was more variable. Finally, the overall foraging effort was reduced compared to variability type I, with the female providing the same amount of krill to the chick in around 27 trips compared to 34 for high krill availability.

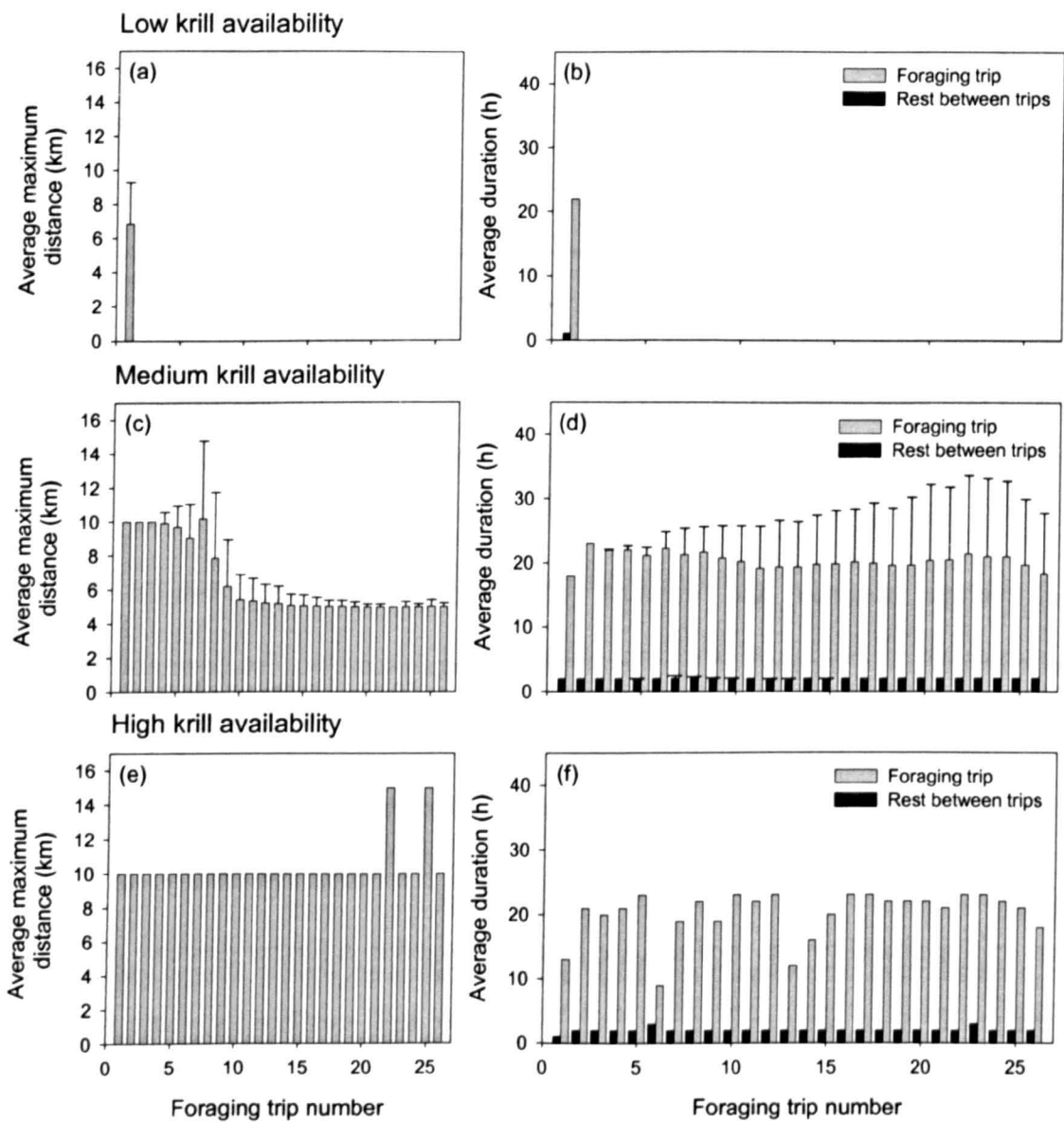


Figure 2.16. The average result for 1000 simulations of the guard stage foraging trips in terms of (a, c, e) maximum distance travelled and (b, d, f) duration of foraging trip with resting time in between (+SD), for simulations with variability type II.

The example trip for low krill availability again shows the female only returning once to the nest, but foraging at a close distance for the remainder of the guard period (Figure 2.17). For high krill availability, foraging trips were more consistent in duration for this scenario compared to variability type I.

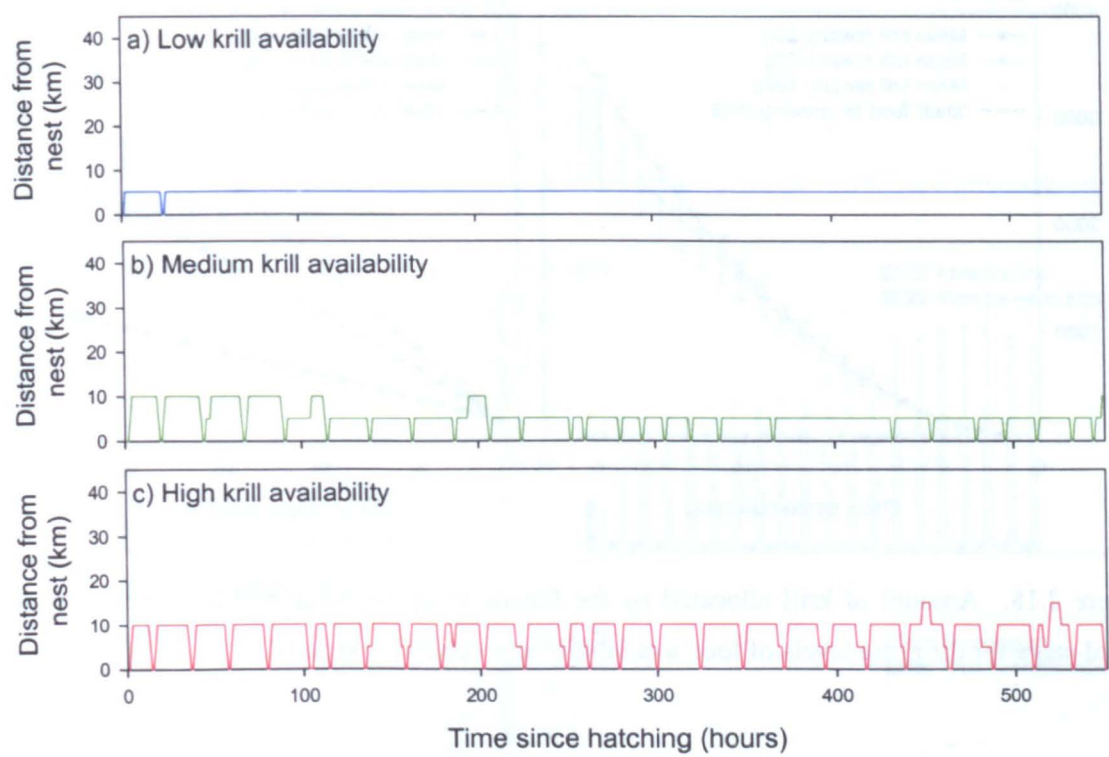


Figure 2.17. An example of the foraging trips of one female for simulations of low, medium and high krill availability, showing the distance from nest over time for variability type II.

Variability type III

The third type of variability was similar to variability type I, where the mean amount of krill was the same at each distance except, in this case, there were only two possible rewards at each distance which became increasingly different with distance from the nest. With this type of variability, the chick did not receive any food when krill availability was low (Figure 2.18). The chick received around the ideal amount of krill for high krill availability, and slightly less than ideal for medium availability, particularly after around day 15. Like the previous scenarios, the amount of food

allocated to the chick was most variable between simulations for medium krill availability. The female ate the ideal amount of krill only with high krill availability, receiving around two thirds of her energetic requirement for medium krill availability, and only one third her requirement for low krill availability.

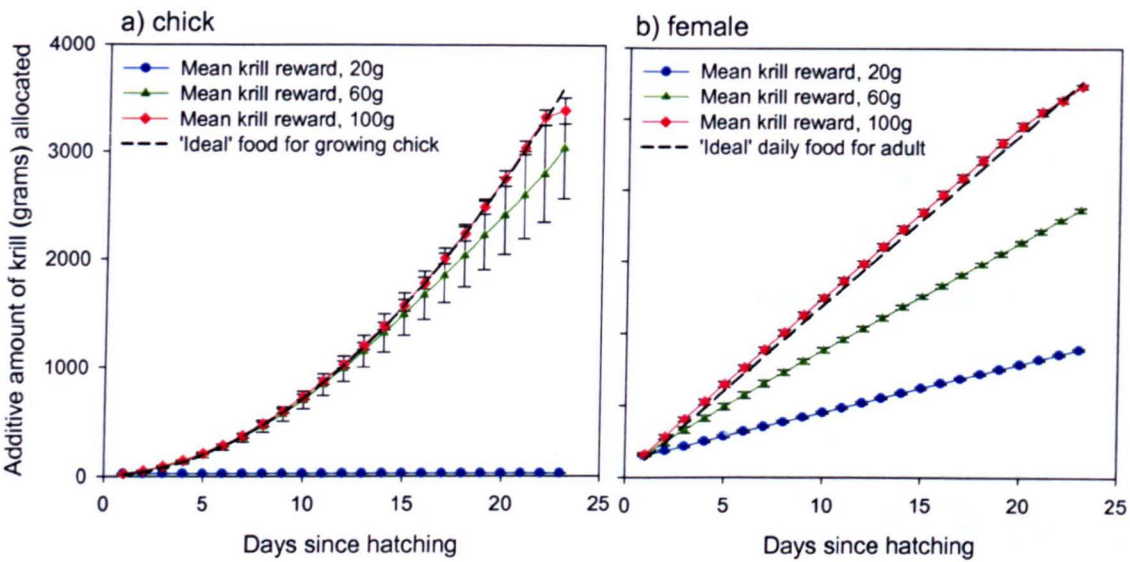


Figure 2.18. Amount of krill allocated by the female to a) the chick and b) herself over the guard stage for differing levels of food availability and variability type III.

The range of foraging trips did not change much over the guard stage for this scenario, with a couple of longer trips at the end of the guard stage when krill availability was high, as in variability type II, and a longer trip at the start with medium krill availability, as in variability type I (Figure 2.19). With low krill availability, there was again only a single return foraging trip to feed the chick. In addition, foraging trips became longer in distance and shorter in duration as krill availability increased, with trips to around 5 km and 25 h for medium krill availability, and 12 to 20 km and 21 h for high availability. Inter-individual foraging trip distance was variable for high krill availability, probably because the variability in krill abundance was higher closer to the nest. Resting time was consistent at around 2 or 3 hours between trips, except the first, which was around

11 hours. The total number of trips with high krill availability was around 24, less than the number of trips for variability types III and I.

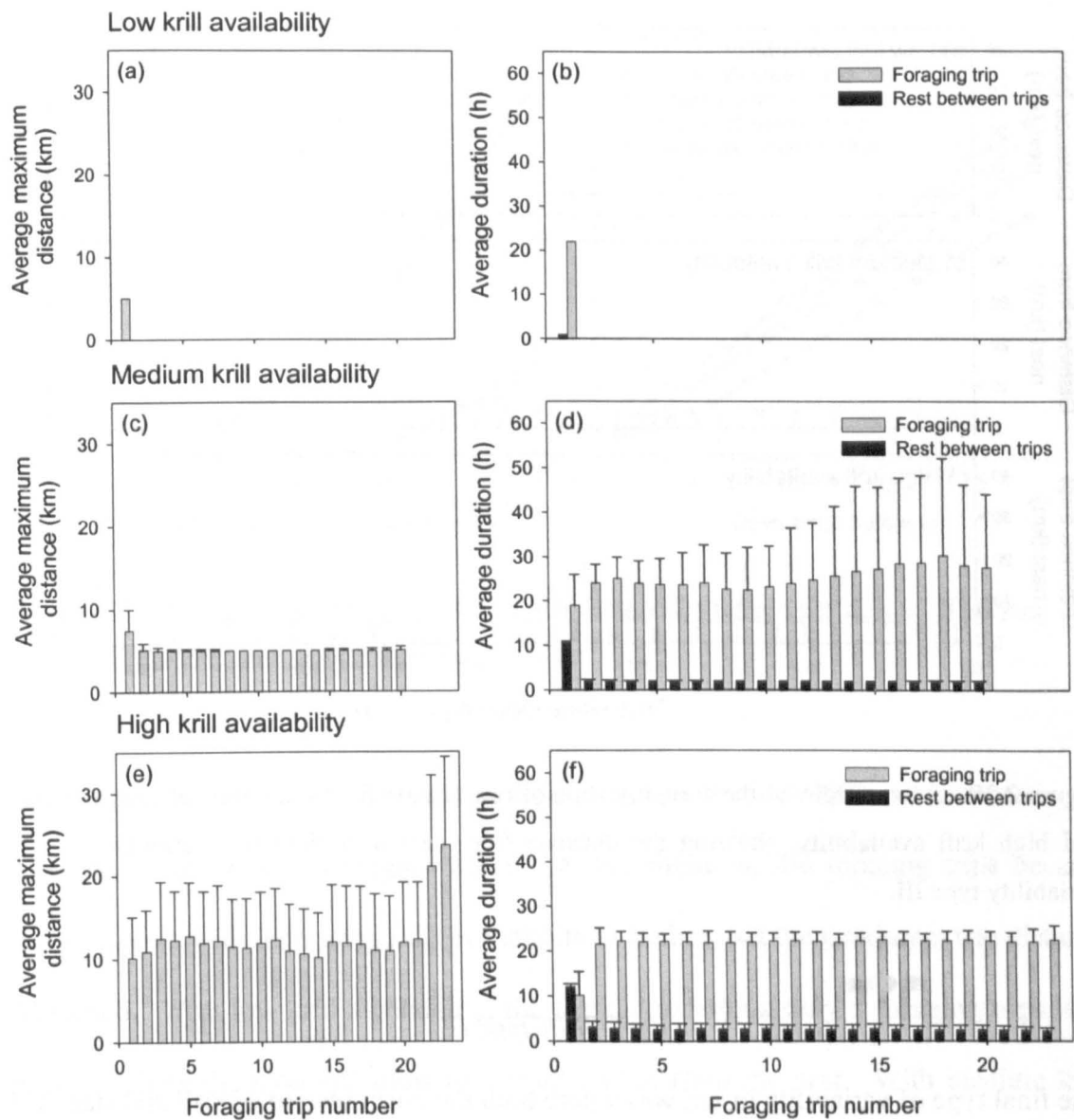


Figure 2.19. The average result for 1000 simulations of the guard stage foraging trips in terms of (a, c, e) maximum distance travelled and (b, d, f) duration of foraging trip with resting time in between (+SD), for simulations with variability type III.

The example trip for low krill availability again shows a situation analogous to chick abandonment as the female only returns once to the nest during the guard stage, but forages close to the nest for the remainder (Figure 2.20). In addition, the difference in foraging trips between medium and high krill availability can be seen primarily in the

consistently low distance of trips with medium krill availability compared to longer ranging and more variable ranging trips with high availability.

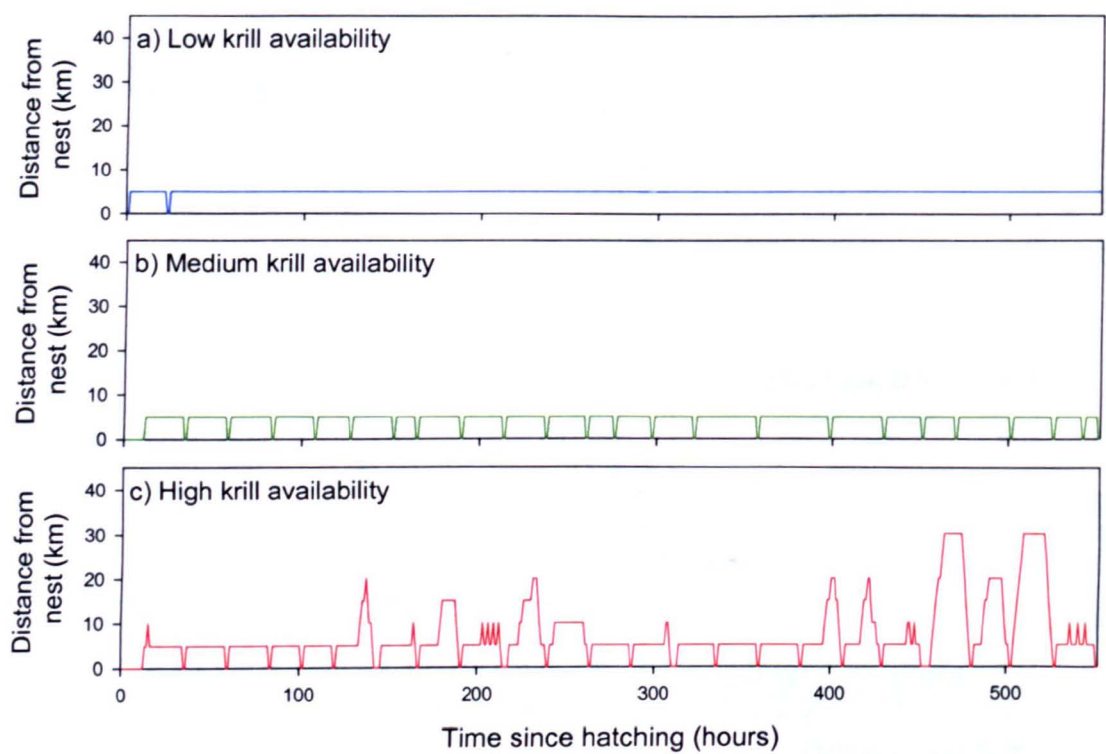


Figure 2.20. An example of the foraging trips of one female for simulations of low, medium and high krill availability, showing the distance from nest over time for a simulation with variability type III.

Variability type IV

The final type of variability tested was where both the mean reward of krill and standard deviation around the mean increased with increasing distance from nest. In this scenario, the chick received almost exactly its ideal amount of food for all simulations except when krill availability was low (Figure 2.21). Here, the chick received no food until day 15, after which the female delivered meals at a constant rate. The difference that low, medium and high krill availability had on the female was linear, with a difference of around 20% of the ideal energetic requirement between each of the simulations. With high krill availability, the female ate around 10% more than the ideal

amount, and for medium and low krill availability, she ate 10% to 30% less than the ideal respectively.

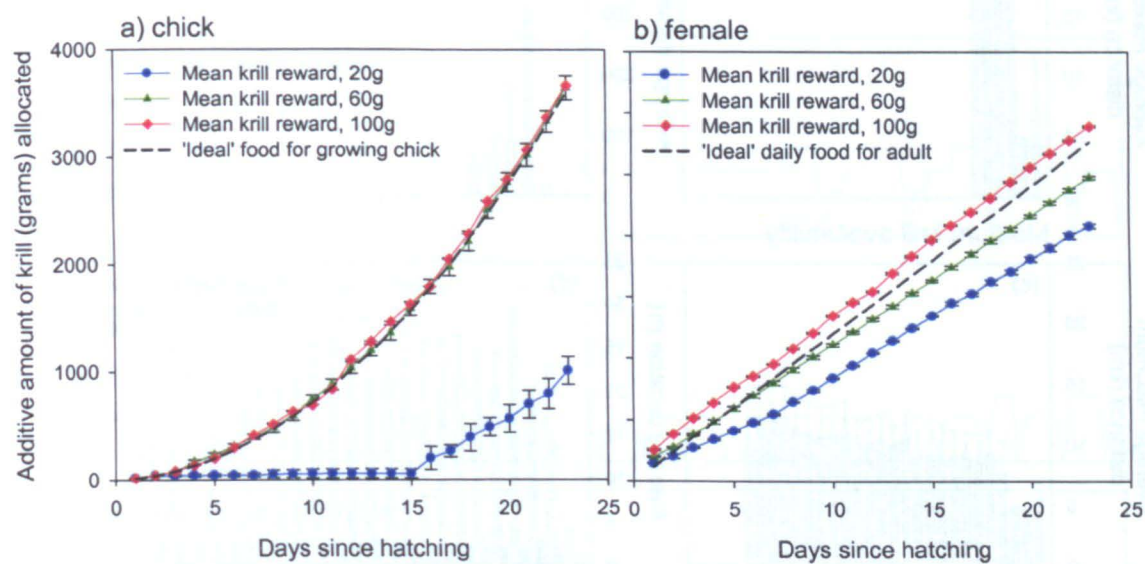


Figure 2.21. Additive amount of krill fed to a) chick and b) female per day, with varying krill availability for simulations with variability type IV.

The foraging trips of the female for this type of variability were different to those in the other described scenarios (Figure 2.22). In this situation, the foraging trips became more frequent with increasing krill availability as before, but the maximum trip distance decreased. With low krill availability, the female undertook only 5 foraging trips, one of a very long duration and most to around 20 km from the nest. With medium krill availability, the average trips were more frequent and closer to the nest; initially with a maximum distance of around 5 km and increasing over time to around 10 km from nest as the demands of the chick increased. With high krill availability, trips were short, consistently to 5 km from nest. Although the trips varied in duration, there was no variability between individuals for each simulation of the model. This could be because the krill supply at 5 km from nest was sufficient to feed both the female and the chick, and also because there was very little variability in the krill reward at 5 km from nest, with variability increasing with distance.

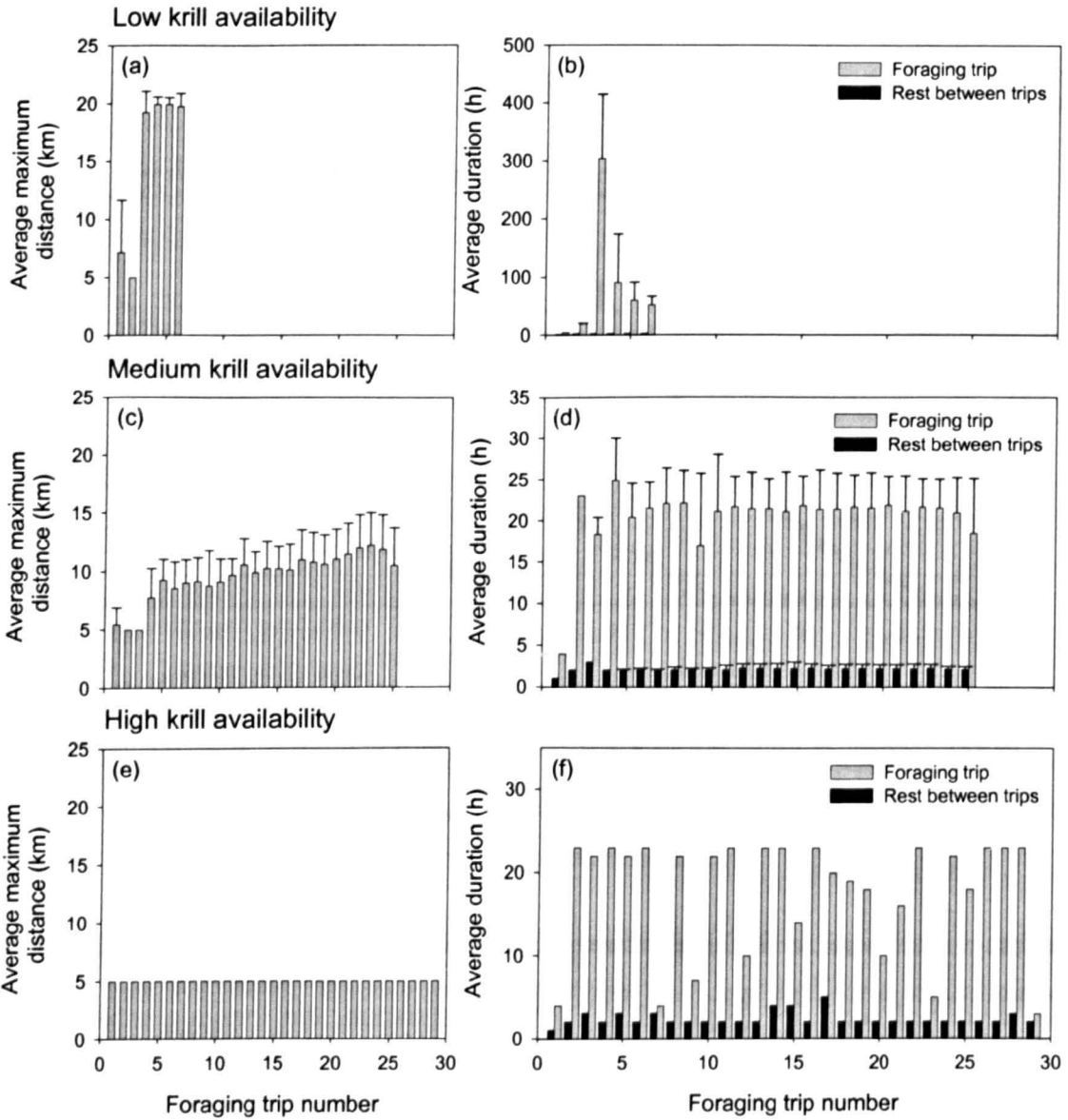


Figure 2.22. The average result for 1000 simulations of the guard stage foraging trips in terms of (a, c, e) maximum distance travelled and (b, d, f) duration of foraging trip with resting time in between (+SD), for simulations with variability type IV.

The example trip demonstrates the difference between this type of variability and the other scenarios tested (Figure 2.23). With low krill availability, there was more than one return foraging trip to the chick, with the female returning around 7 times. In this instance, it was possible to travel further to secure a large enough meal to feed the chick on return because the krill reward increased with distance from nest, unlike the previous scenarios (variability types I, II and III). In addition, the situation for medium and high

krill availability was reversed, with longer ranging and more variable trips for medium krill availability, compared to consistent short trips with high krill availability.

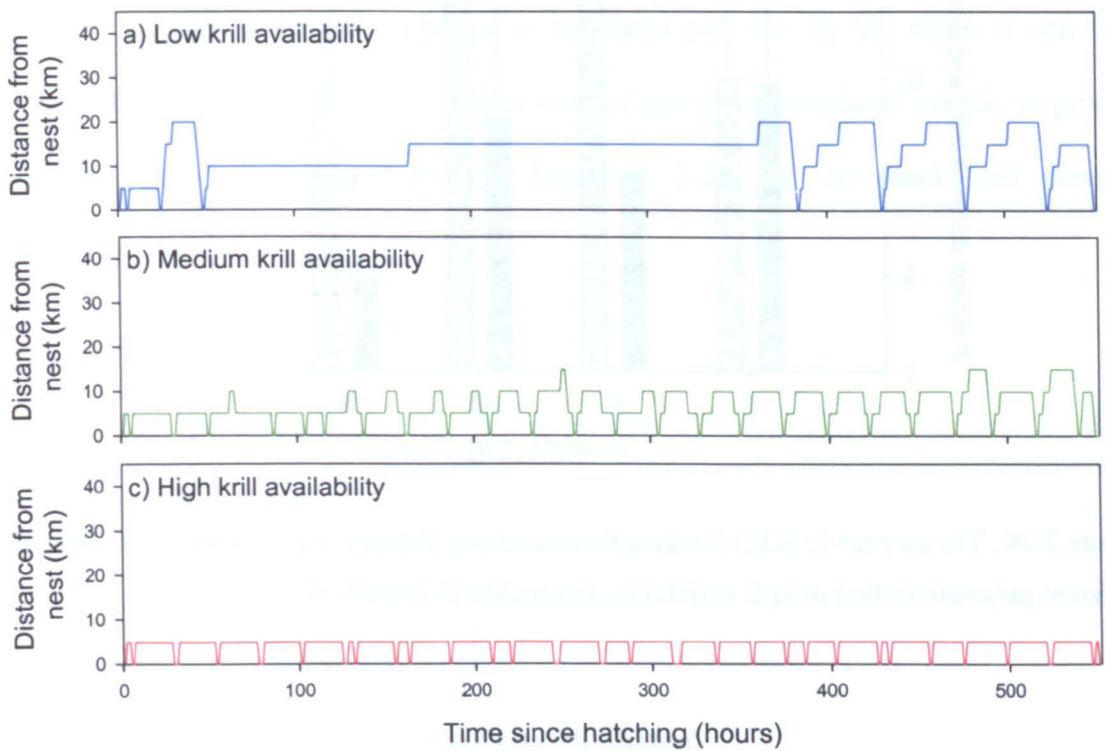


Figure 2.23. An example of the foraging trips of one female for simulations of low, medium and high krill availability, showing the distance from nest over time with variability type IV.

The effects of krill variability on foraging trips

The foraging trip distance and duration were both most variable for models with krill variability types I and III (Figure 2.24). This is most likely because, for both of these scenarios, krill variability decreased linearly with increasing distance from nest: less rapidly than the exponential decrease in variability for type II and the gradually increasing variability in type IV. Even though the mean reward did not vary with distance for types I, II and III, the average foraging distance was still further than the closest distance to the nest (5 km). This means the female was maximising fitness by travelling to a supply of krill that was less variable and more reliable, at the cost of increased travelling time.

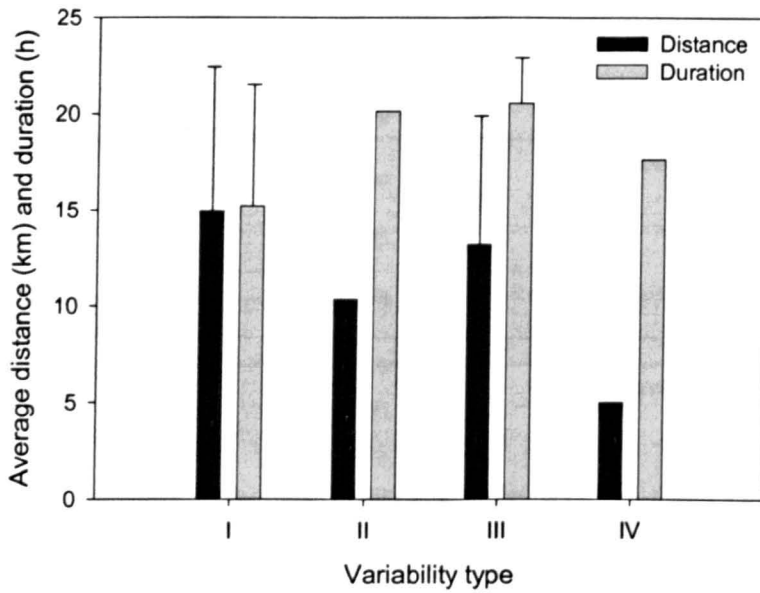


Figure 2.24. The average (\pm S.E.) foraging trip maximum distance and duration for models with different parameterisation of krill variability, and high krill availability.

Sensitivity analysis

This section deals with the sensitivity of the model results to changes in the parameters specifying the maximum stomach capacity of the female and chick, f_{max} and ch_{max} respectively, the maximum distance the female can travel from the nest, d_{max} , and costs to fitness, c_f and c_{ch} (see Table 2.2). The results tested are the energetic levels of the female and chick, and the foraging trip result in terms of distance traveled, duration and resting time between trips. The following equation gives the calculation of sensitivity, by dividing the percentage change in the result by the percentage change in the variable tested. This gives a measure of the change in the result relative to the change in the variable.

Equation 2-19
$$Sensitivity = \frac{\Delta result}{\Delta parameter} \%$$

The sensitivity test altered the energy accumulated per day by the chick X and the female f . This was divided by the ideal amount of energy accumulated per day to give a ratio, as detailed Equation 2-20 and Equation 2-21 for the chick and female respectively.

Equation 2-20
$$Ebalance_{ch} = \frac{X}{ch_{day}}$$

Equation 2-21
$$Ebalance_f = \frac{f}{f_{day}}$$

This ratio was averaged over the 23 days of the guard period for both the chick and the female.

Both the chick and the female were most sensitive to changes in the parameter specifying the fitness cost, although this was highly variable. Both were also sensitive to changes in the maximum stomach capacity of the chick. Changes to the maximum stomach capacity of the female f_{max} or maximum distance from the nest d_{max} had little effect on model results.

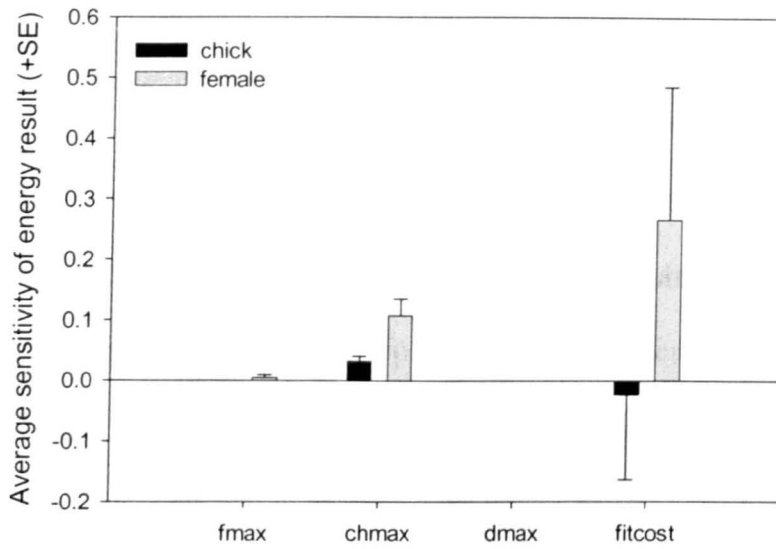


Figure 2.25. The sensitivity of the energy result for both the chick and parent in response to changes in parameter values.

Sensitivity of the foraging trips to changes in parameter values

Foraging trip characteristics were more sensitive than energy status to changes in parameter values (Figure 2.26). Like energy status, the amount of time spent resting between foraging trips was most sensitive to changes to the fitness cost of the female or chick having an empty stomach. However, both foraging trip distance and duration were most sensitive to changes in the parameter specifying the maximum stomach size of the chick. Foraging trips were not sensitive to changes in the maximum distance from nest d_{max} or the maximum stomach capacity of the female f_{max} .

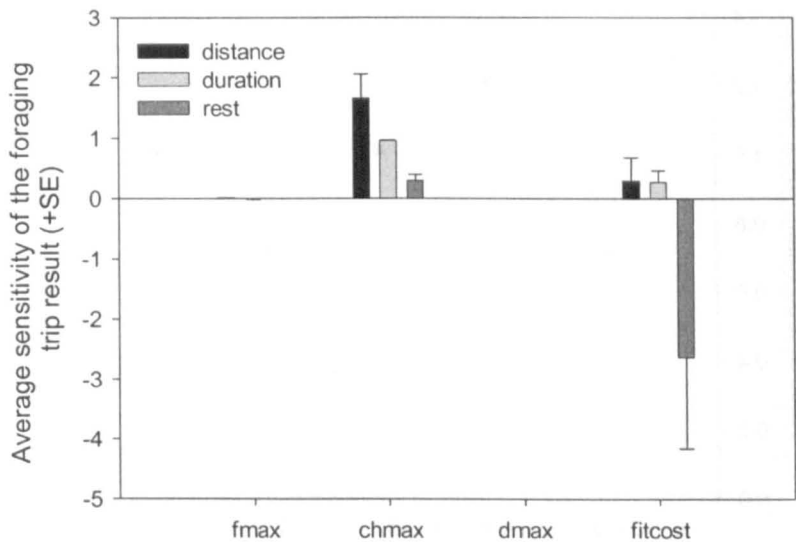


Figure 2.26. The sensitivity of the foraging trip response in terms of trip distance, duration and resting time between trips.

Sensitivity of model predictions to fitness costs

Here, the sensitivity of the model to relative fitness costs of having an empty stomach were tested. Figure 2.27 shows the energetic response of the female and chick to changes in the fitness cost parameter. When there was no cost for either the female or chick going without food (0,0), they both received much less than their ideal requirement of food for the guard stage. When there was only a cost for the chick (1,0), the chick received around 20% more than its ideal amount of krill but the female still received less than half of hers. With an equal fitness cost for both the female and the chick (1,1) or for further changes in the parameter where there was a cost associated with both the female and the chick, the chick received the ideal amount of krill and the female received around 80%.

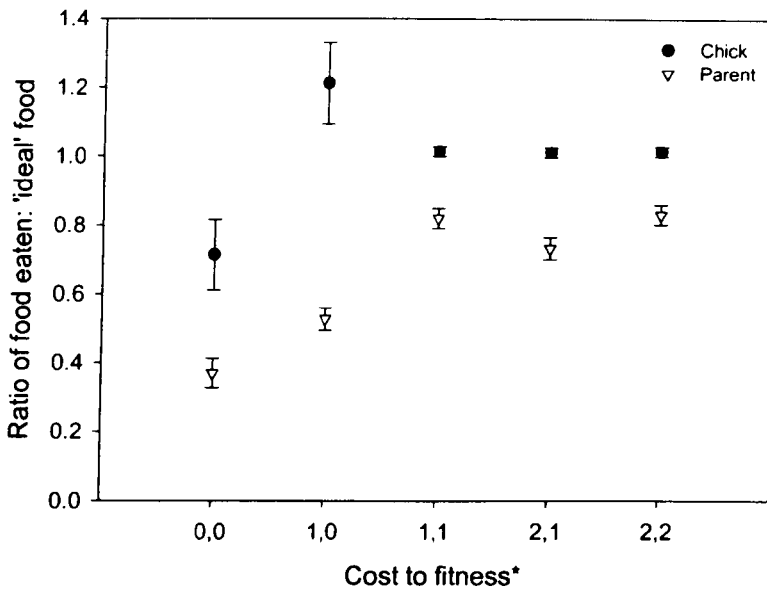


Figure 2.27. The average effect (\pm S.E) of changes in fitness cost on the final energy result of the female and the chick. Cost to fitness of having an empty stomach shown as (c_{ch} , c_{fi}) for the chick and female respectively. See (Table 2.3) for an explanation.

When there was no cost for either the female or chick going without food (0,0), the foraging trip distance was more variable, around 15 to 20 km from nest (Figure 2.28). With only a cost for the chick going without food (1,0), foraging trips became closer than 10 km from the nest. With an equal cost to fitness for both the female and the chick (1,1), foraging trips were around 25 km from the nest. However, when the cost to the chick was greater than to the female, the trips became closer to the nest again.

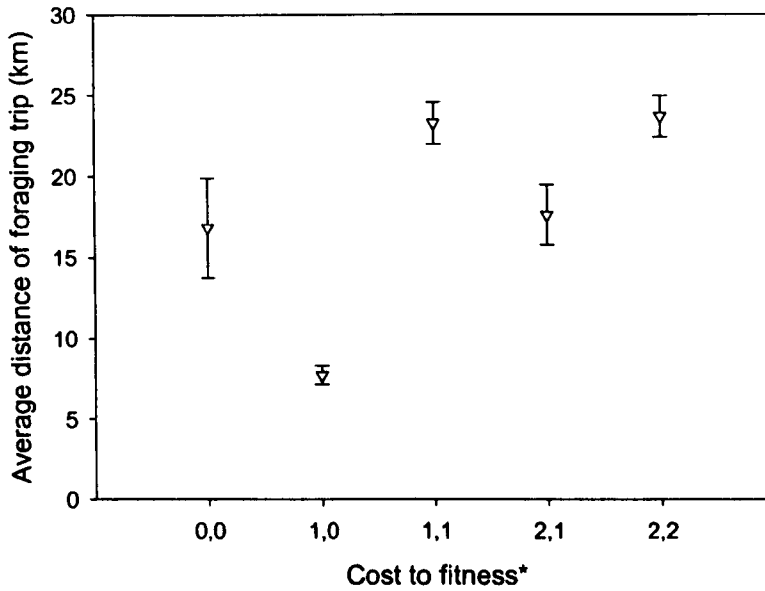


Figure 2.28. Effect of changes in the parameter specifying fitness cost on the average distance (\pm S.E.) of foraging trips for the female. Cost to fitness of having an empty stomach shown as (c_{ch}, c_f) for the chick and female respectively. See (Table 2.3) for an explanation.

With no fitness cost for the female or chick (0,0), trip duration is less and rest duration is much greater than when there is an equal cost to fitness for the female and chick (1,1) (Figure 2.29). When there is only a cost associated with the chick (1,0), both resting time and trip duration are less than with no cost at all (0,0). Any cost to the chick reduces parental resting time to just 2 time periods (2 h) in the model. However, further changes to the fitness parameter after there is some cost to both the female and the chick (1,1), (2,1), (2,2) have no effect on the duration of trips and resting time in between. Trip duration is constant at around 22.5 hours and rest duration at around 2 or 3 hours. Foraging trips were approximately daily for the best estimate model.

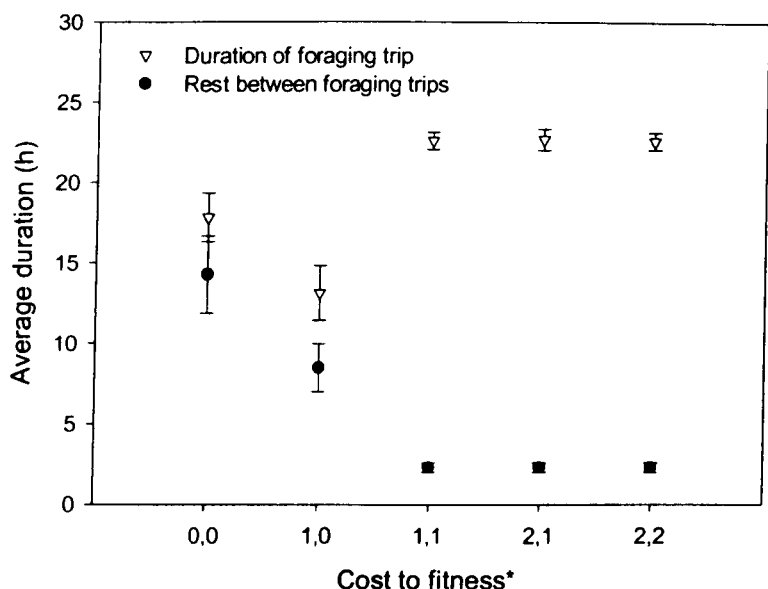


Figure 2.29. Effect of changes in the fitness parameter on average duration of foraging trips and average resting time in between. Cost to fitness of having an empty stomach shown as (c_{ch} , c_f) for the chick and female respectively. See (Table 2.3) for an explanation.

DISCUSSION

Fitness costs

When the fitness cost to both the female and chick were equal, the model results were similar to those in the field. In a year with average food conditions, the chick grows at a rapid rate (Brown, 1987a) and females lose on average 14% of their body weight during the guard stage (Barlow and Croxall, 2002a) compared to around 20% in the current model. The results suggest that the female does not just try to maximise the amount of krill fed to the chick, but also attempts to minimise the time that she or the chick goes without food.

While it is intuitive that the female must consider both the condition of herself and her offspring when making decisions, how she should balance her own condition against that of the chick, or current versus future reproductive success, is unknown. In a year

with average food conditions, the chick grows to the size of around 1300 g during the guard stage, and the female loses on average 14% her body weight, or around 530 g (Barlow and Croxall, 2002a; Brown, 1987a). In the model, fitness was considered in terms of total penguin weight in relation to daily energetic requirements; increasing when the chick was fed its daily requirement and therefore enough to grow at the ideal rate, and decreasing when either the chick or female did not receive their daily requirement, therefore decreasing in weight. This fitness was realised with each time step of the model, in other words, fitness accrued at each time step (Mangel and Clark, 1988). This type of fitness function is used for example for the oviposition behaviour of insects encountering and laying eggs in hosts in each period (Mangel and Clark, 1988).

The model predicted that neither the chick nor female received enough krill to satisfy their energy demands when a cost to fitness of having an empty stomach was not included. When a cost was included only for the chick, the chick received more than its requirement of krill, with the female receiving only half. In addition, resting time for the female was reduced to only 2 hours. This is because the female attempted to maximise the amount of krill allocated to the chick without considering her own condition at all. With an equal cost for both the female and chick having an empty stomach, the chick received its energy requirement and the female received on average around 80% of hers. However, further changes to the fitness parameter did not have a noticeable effect on energy levels. Testing the sensitivity of the model, changes to the fitness parameter had the greatest effect on resting time. This is because, when there was no fitness cost, the female was under less pressure to provide a daily meal for the chick, so stayed at the nest for longer between trips keeping the chick topped up with food.

Energy and nest failure

In the model, the chick received around 100% of its energy requirement of krill in all conditions except the lowest availability of krill, indicating there was some threshold amount of krill availability, above which it received its energy requirement, below which it failed. Below the threshold, the situation was analogous to nest failure, although there was no parameterisation of chick death in the model. In contrast to the chick, the availability of food had a mostly linear effect on the amount of food the female allocated to herself, receiving 100% of her energy requirement only with high krill availability. A situation analogous to nest failure occurred for most simulations with low krill availability, where the female made only one or a few return foraging trips, foraging for the rest of the guard stage close to the nest but not returning to feed the chick. This is because, when the krill resource was variable, the female would have digested the small amount of krill in her stomach by the time she returned to the nest. She continued to forage close to the nest where the possibility of a large reward was small but greater than that further out, and was the only possibility that she could return with a meal big enough to feed the chick. These results suggest that the female keeps up a constant reward to feed the chick at the cost of her own starvation, down to a certain point or threshold at which the female abandons provisioning to the chick and feeds herself.

The energy result was most sensitive to changes in the parameterisation of both the maximum stomach capacity of the chick and the cost to fitness associated with a failure to meet energy demands. This highlights the importance of obtaining accurate estimates of meal sizes and stomach capacities of chicks during the guard stage, although

unfortunately this is when nest disturbance by field-workers is most likely to have a negative effect on chick survival and growth (Trathan personal obs.). In addition, this finding stresses the importance of relying on these results only for qualitative predictions, because a factor such as the fitness cost is inherently hard to parameterise.

Parents must make decisions based on both their own physiological state and the state of their offspring to maximise both current and future reproductive success (Clark and Mangel, 2000; Williams, 1966). This means that parental care is only beneficial when it increases the probable survival of the offspring without incurring too great a cost to the parents (Clutton-Brock, 1991). In the field, there are indications of a threshold level of parental expenditure for macaroni penguins, related to prey availability, below which the chick fails, and above which there is no significant increase to chick growth (Barlow and Croxall, 2002a; Lynnes et al., 2004). This is potentially most likely to happen during the guard stage when the female is under pressure to provide regular meals of increasing size (Barlow and Croxall, 2002a). The fact that she loses on average 14% of her body weight during this stage is an indication of her expenditure to the current reproductive event (Barlow and Croxall, 2002a), however there is no record of an adult macaroni penguin dying of starvation during breeding or moult (Williams et al., 1992). Therefore, there must be a point at which the female abandons the chick in order to maintain her own condition, but the threshold or conditions for abandonment are unknown. The point of abandonment is possibly based on body weight (or condition), as demonstrated in parent Antarctic petrels, *Thalassoica antarctica*, and Kittiwakes *Rissa tridactyla* in Shetland, that give priority to their own state when their body mass is low (Hamer et al., 1993; Varpe et al., 2004), which can be affected by low food conditions or may also be dependent on other factors such as foraging skills (Olsson,

1997). I predict chick abandonment in the model due simply to the female not being able to obtain a meal that is large enough to avoid being fully digested before arriving at the nest.

Foraging trips

Predicted interannual differences in trips for a simple model

Conditions for a foraging penguin can change from year to year in terms of absolute availability as well as variability in krill abundance. The former is discussed here and the latter in the following section. In the simplest parameterisation of the model, where krill availability increased linearly with distance from nest, predicted foraging trips generally increased in distance and decreased in duration with increasing krill availability. However, duration of foraging trips was approximately the same for levels of medium and high food availability. The total number of foraging trips was therefore greatest for simulations of both high and medium krill availability and lowest for simulations of low krill availability. In years of high krill availability, it was beneficial for the female to travel further from the nest to secure a meal that could satisfy the requirements of both the chick and herself. Because krill availability was high, she was able to obtain a large meal in a short amount of time, which reduced the foraging trip duration. With medium krill availability, the model predicted foraging trips closer to the nest, which meant that the chick received its energy requirement, but the female received less than the ideal requirement of krill. With both medium and low krill availability, the benefit of an increased krill reward further from the nest did not outweigh the cost of travelling time without feeding, hence, the trips were closer to the nest. This represents a complex prediction, but reflects the complex problems faced by the penguins.

Few studies record both foraging trip range and duration for penguins, particularly in relation to prey availability. However, a number of different studies and techniques provide evidence for interannual changes in foraging trips. Earlier studies on penguin foraging trips only recorded the duration of foraging trips, either manually recording the return of the bird to the nest, or by using time depth recorders. Overall, these studies report increasing trip duration with decreasing prey availability. A number of species demonstrate this trend, including macaroni and gentoo penguins at South Georgia (Barlow et al., 2002; Croxall et al., 1999), Humbolt penguins, *Spheniscus humboldti*, in Chile (Hennicke and Culik, 2005), and Adélie penguins, *Pygoscelis adeliae*, at Bechervaise Island and Signy Island (Irvine et al., 2000; Lynnes et al., 2002). Additional evidence for the trend comes from other krill-dependent predators such as Antarctic fur seals, which breed at similar locations to macaroni penguins at South Georgia and also rely on Antarctic krill, and that forage for longer in years of low krill availability (Boyd et al., 1994). However, there is evidence to the contrary, that macaroni penguins appear reluctant to increase foraging trip duration at the expense of meal size (Croxall et al., 1999). In the current model, this is demonstrated by the female not taking longer trips during years of medium krill availability compared to high, suggesting that differences in trip duration are only noted for particularly low krill years. There is further evidence for this in Adélie and macaroni penguins that seem to have some threshold level of expenditure below which the chick fails, but above which there is little benefit to chick growth (Barlow and Croxall, 2002a; Lynnes et al., 2004). This may relate to when the female is no longer able to maintain a daily foraging trip while also satisfying the minimum energetic requirements for both the chick and herself. I predict increased trip duration of macaroni penguins at South Georgia in years

of low krill availability, but a constant daily foraging trip for medium and high krill availability for a situation where there is no variability in the krill resource.

The development of recent techniques allows the satellite tracking of individuals, providing estimates of foraging trip range as well as duration. However, most of these have so far failed to report an interannual difference in trips, contrasting to the predictions of this model. Trathan et al. (2006) find differences in average foraging concentration of macaroni penguins between years but have not yet related this to krill availability. There are a couple of other studies on the foraging range of macaroni penguins in relation to interannual variability, and both of these report no differences between years (Barlow and Croxall, 2002b; Green et al., 2005). The lack of an interannual effect is probably due to krill availability being similar between years, with Barlow and Croxall (2002b) reporting low krill biomass for both years in their study. In addition, macaroni penguins can switch diet in years of low krill availability (Croxall et al., 1999), which could explain a lack of interannual difference in foraging effort. Finally, differences between the model predictions and the field observations could be because the female in the model was not able to forage and travel at the same time. There are three main types of dives for macaroni penguins: travelling dives, which are mainly underwater; searching dives; and feeding dives (Croxall et al., 1988a). Only a proportion of the overall dives are used for commuting, with periods of feeding and searching approximately evenly spread throughout the foraging trip (Trathan et al., 1998). In the model, the female only had the choice of travelling or feeding dives, each of which were performed separately and for the entire time step of one hour. If a shorter time step were used, or if the female could search while travelling, this may have resulted in a greater return from foraging closer to the nest and thus reduced the

effective cost of travelling time and foraging range of each trip. Central place foraging theory predicts that trip duration will increase with increasing distance to the foraging patch for both single- and multiple- prey loaders unless patch quality increases, as is the case in the model (O'Brien, 1987). Distant patches are not utilised until the time taken to obtain some fixed maximum load increases sufficiently to compensate for the greater travelling time. The current model supports this theory: predicting an extended foraging range in years of high krill availability, due to an increase in the relative balance between foraging reward and travelling time.

There is evidence in other species for increasing foraging effort with decreasing prey availability, such as in Humboldt penguins, yellow-nosed albatrosses and Antarctic fur seals (Boyd, 1999; Culik and Luna-Jorquera, 1997; Hennenke and Culik, 2005; Pinaud et al., 2005). In addition, Adélie penguin parents travel to more distant sites and chinstrap penguins increase provisioning frequency as the season progresses when rearing a chick (Jansen et al., 2002; Kato et al., 2003). Adélie penguins increase foraging trip duration with low food availability (Watanuki et al., 1993) as do guillemots which have shorter trips when food is more available (Hatchwell, 1991). There are many other examples in the literature for foraging trip changes with food availability (Ainley et al., 2003; Barrett and Krasnov, 1996; Daunt et al., 2002; Furness and Tasker, 2000; Hamer et al., 1993; Litzow and Piatt, 2003; Rindorf et al., 2000; Suryan et al., 2000; Suryan et al., 2002).

Predicted interannual difference in trips for a model with variability

Changes in the variability of the krill resource can also have an effect on penguin foraging behaviour. With variability in the krill resource, where the mean reward was constant but variability around the mean decreased with increasing distance from the

nest (variability type I, II, III), the model predicted that the female travelled to a distance where the krill supply was more reliable, at the cost of extended travelling time. This only occurred for simulations of medium to high krill availability, suggesting that the female could only afford the cost of increased travelling time when krill availability was sufficiently high. With low krill availability, the fitness benefit of a more reliable source of krill was outweighed by the cost of travelling time for such a low reward. The only exception to this pattern was in simulations where both krill availability and variability increased with increasing distance from nest (variability type IV). In this scenario, the female foraged closer to the nest as krill availability increased, because she could obtain both a large enough and reliable enough reward of krill close to the nest. Variability in foraging trip distance and duration was greatest for scenarios type I and III, because the optimal foraging distance for these scenarios was also a distance where krill variability was relatively high compared to the model scenarios of types II and IV.

Both the foraging trip duration and range were most sensitive to changes in the maximum stomach capacity of the chick. This is because the maximum stomach capacity of the chick could effectively increase or decrease the maximum time between meals, before there was a cost to fitness. With potentially higher maximum foraging trip duration, the female would be free to use a greater travelling time in each foraging trip, therefore being able to travel further to either a more reliable supply of krill or a greater reward of krill.

There is evidence in the field that macaroni penguins in the guard stage travel straight out to the shelf break each year, with their average foraging range over 7 consecutive

years showing an almost straight line from Bird Island, South Georgia, to the shelf break (Trathan et al., In Press). There is further evidence for this type of behaviour in the closely related rockhopper penguins, *Eudyptes chrysocome*, that are believed to commute a roughly straight line between the breeding colony and the slope of the continental shelf at the Falkland Islands (Putz et al., 2003). These results suggest that both macaroni and rockhopper penguins (both *Eudyptes* species) prefer to head straight to a distant point where krill availability is more reliable, rather than spending time searching for a more patchy krill resource close to the colony. The krill resource is likely to be less reliable on shelf because, although krill are located in higher concentrations here than off shelf, they are more likely to be located in tight swarms as a defence mechanism against a higher density of predators (Hamner and Hamner, 2000; Hunt et al., 1992; Ritz, 1994). I predict that macaroni penguins prefer to travel straight to the shelf break, and that this pattern will be demonstrated particularly in years of high krill availability when the reward is high enough to offset the cost of travelling further. This result also highlights the potentially important effect of krill swarm density on penguin foraging decisions.

Krill aggregations are variable on temporal and spatial scales due to a number of factors, including their diel vertical migration (Godlewski, 1996), swarming behaviour (Ritz, 1994), and transportation by currents (Hofmann and Murphy, 2004; Murphy et al., 1998). While there is a general understanding of the causes of krill variability, there is little understanding about how this affects availability to a visual predator. Krill in a swarm can reduce predation by increased vigilance, or by adopting group defensive tactics, such as evasion and dilution (O'Brien, 1987; Ritz, 1994), therefore potentially reducing availability to predators. On a spatial scale, this would imply that krill may

aggregate more densely in the presence of predators, and indeed there is some evidence for this (Zhou and Dorland, 2004), which is investigated in the following chapters. From this, it follows that krill may aggregate more densely close to an island where predators are abundant. This is the basis for the first three types of variability tested in the model, where krill on shelf with a high concentration of predators are more likely to be located in dense swarms, therefore increasing their patchiness and variability. Further from the island, where predator concentration is reduced, krill are more likely to be located in less dense aggregations, distributing themselves more evenly on a spatial scale.

The final type of variability tested was where the mean reward of krill increased with increasing distance from the nest, and variability around the mean increased in proportion to the mean. In terms of concentration, krill are believed to be most concentrated at the shelf break (Trathan et al., 2003). This means that, with increasing distance from shore, krill availability is likely to increase until the shelf break, and then decrease off shelf. I predict that penguins will respond differently to different types of krill variability between years, and suggest that it may be possible to determine a broad pattern of krill availability given the ability to track macaroni penguins and to compare foraging trip ranges and durations.

Predicted changes in trips over the guard stage

Increasing demands of the chick over the guard stage, as well as possibly decreasing condition of the parent at this time, may also affect the foraging trips of the parent penguin. Generally, the model predicted that the female took more risks in her foraging choices towards the end of the guard stage. This was demonstrated mainly for medium

krill availability for models with variability type I, II and III, where the foraging trips of the female tended to decrease in distance but not duration over time. Foraging closer to shore meant that the krill availability was less reliable, but there was the possibility of a larger meal, which was needed for increasing chick demands, and also meant the female could return more often to feed the growing chick. With high krill availability and variability type II, the model predicted the opposite trend, with a couple of trips to a greater distance towards the end of the guard stage. It is possible that with increased chick demands and higher availability of food it was more important to obtain a reliable meal at this stage. It is also likely that duration did not increase over time because the female was constrained by a need to feed the chick daily, to avoid the fitness cost from the chick having an empty stomach.

There is evidence that the foraging effort of the parent penguin increases as chicks become older. Croxall *et al.* (1993) reported that macaroni penguins were more likely to undertake longer, overnight, foraging trips later in the guard stage. A similar pattern is reported for Adélie penguins, *Pygoscelis adeliae*, which travel to a further distance as chicks age (Kato *et al.*, 2003). However, the reverse pattern has also been observed for macaroni penguins at Heard Island, with diving activity during the day declining with the progress of the season (Green *et al.*, 1998). It is unknown whether increasing foraging effort with time is due to an inshore depletion of stocks, increasing chick demand or the idea that older chicks can withstand empty stomachs for longer (Croxall *et al.*, 1993; Kato *et al.*, 2003). Chicks may be able to go longer on empty stomachs due to the build up of fat reserves that can have a buffering effect on meal delivery time, as seen in other birds such as raptors (Brodin and Jonsson, 2003). I predict an increase in foraging effort, reflected in the maximum distance not the duration of foraging trips,

over time, only when krill availability is high. I also predict a reduced foraging range over time when krill availability is medium, due to an increase in the relative balance between travelling costs versus a more reliable reward of krill. Increasing chick demands, not the ability of the chick to go for longer without food, bring about the change in effort over the guard stage. However, the ability of chicks to survive for longer between meals is likely to have an effect on foraging trips.

Resting

Resting time between trips was generally around two to three hours. This result was constant despite changes in krill availability and other parameters, but was sensitive to changes in the parameter specifying fitness costs. The only exception was one or two extended periods of rest at the start of the guard stage in one of the scenarios tested (variability type IV). As there was no reduction in metabolism while resting in the model compared to foraging at sea, the female only rested at the nest in order to top the chick up with food every hour until her stomach either was empty or reached a critical low level of food. In addition, resting duration was constant through changes in the model, which meant that birds were leaving the nest at different times of day. This suggests that the difference in foraging success between day and night may not have been high enough, or that the female was travelling through the night. Resting duration in the model was most sensitive to changes in the fitness cost associated with failure to meet energy demands for the female and chick.

During the guard stage, Barlow and Croxall (2002a) estimated that the female provided on average 17 meals to the chick over 23 days, with an average trip duration of 16 hours. Although there were some overnight trips towards the end of the guard stage,

this suggests a resting time significantly greater than that predicted by the current model. In the field, while penguins forage mostly during daylight hours, the occurrence of overnight feeding is not uncommon (Croxall et al., 1993; Green et al., 2003; Jansen et al., 1998; Wilson et al., 1993). Therefore, when the female is the sole providing parent during the guard stage, she commonly returns to the nest at night to rest after undertaking a daily foraging trip. Although well documented, it is difficult to parameterise the benefits and costs to resting, which may be more significant than a change in metabolic rate. Green *et al.* (2002) reported a generally higher metabolism of macaroni penguins at sea of 9 W kg^{-1} compared to 6.3 W kg^{-1} at the nest. However, another study on emperor penguins suggests that the metabolic rate while diving was similar to their metabolic rate when out of the water during their daily activity period, although this could be due to a decline in the cost of swimming with increasing size (Nagy et al., 2001). I predict a constant resting time throughout the guard stage in response to changes in krill availability and variability.

SUMMARY OF FINDINGS

- A model where the female maximised the amount of food to the chick while minimising the time that she or the chick went without food provided predictions most similar to those from the field.
- Chick abandonment was predicted in the model simply because of the female not being able to obtain a meal large enough to avoid it being fully digested before arriving at the nest.
- Generally, with increasing krill availability, foraging trip distance increased and duration decreased, due to changes in the relative balance between the reward from foraging and the cost from travelling.

- The model predicts that macaroni penguins will endure the cost of travelling further from the nest to obtain a more reliable meal of krill, even if the mean reward does not change with distance from nest.
- The effects of krill variability in the model suggest that swarm density is likely to have an effect on penguin foraging decisions.
- Trip distance increased towards the end of the guard stage when krill availability was high.
- In contrast, trip distance decreased for lower krill availability, meaning that the female was foraging for a less reliable krill reward as chick demands increased. Foraging closer to the nest could arise as a result of an increased probability of a high reward here, with the cost of increased chance of a low reward, or just to reduce travelling time.
- Resting time was constant through changes in krill availability and over the guard stage.

FUTURE VALIDATION

The following experiments are recommended for testing the predictions made by the present model:

- Monitoring the body mass of female macaroni penguins during the guard stage in a year of low krill abundance to determine if there is a threshold level of body condition below which the female will abandon the chick.
- Combining interannual satellite tracking data with krill density estimates over years of varying krill availability to determine if foraging trips increase in distance and decrease in duration for years of high krill availability.

- Satellite tracking combined with nets and acoustics to determine if macaroni penguins travel straight to an area where the supply of krill is more reliable rather than searching close to the nest where krill may be more patchy.
- Further satellite tracking experiments to determine if foraging trips change over the course of the guard stage in response to increasing chick demands.
- Further metabolic experiments on females at the nest and at sea while chick rearing to determine if there is a benefit to resting at the nest.
- If possible, long-term experiments monitoring the growth of chicks during the guard stage and comparing with krill survey data to determine: if there is a threshold krill availability, below which the chick fails, above which growth is normal; and at what point of starvation the chick will die.

3.

Effects of optimal behaviour patterns on local-scale distributions of krill around South Georgia

INTRODUCTION

Antarctic krill, *Euphausia superba*, are of central importance in Antarctic ecosystems (Hamner and Hamner, 2000). This is particularly the case in the region of South Georgia, where they comprise over half the overall zooplankton biomass (Atkinson et al., 2001). In this region, productivity in terms of both phytoplankton and zooplankton far exceeds that elsewhere in the Southern Ocean, with krill the major link between primary production and higher trophic levels (Atkinson et al., 2001; Hofmann and Murphy, 2004; Zhou and Dorland, 2004). Large colonies of breeding seals and seabirds are dependent on krill for their breeding success at South Georgia each summer (Atkinson et al., 2001; Croxall et al., 1999; Reid et al., 2002). Additional pressure on the krill resource derives from the recent establishment of a winter krill fishery in the region (Atkinson et al., 2001; Everson and Goss, 1991; Mangel and Switzer, 1998). The summer season is a crucial time of year for krill, when growth rates may be up to twice that in the winter, and additional energy input is needed for reproduction (Hofmann and Lascara, 2000; Quetin et al., 1994). Given the importance of krill in this system, it is essential to understand factors affecting krill abundance and distribution at this time of year.

Krill as a resource are variable in space and time. This is due to a number of factors: they migrate vertically in the water column (Godlewska, 1996); they are found in swarms and aggregations of varying size and density (Marr, 1962); and they can be transported long distances by currents (Hofmann and Murphy, 2004). Each of these factors is in turn affected by changing conditions, such as phytoplankton levels, predation levels and current velocities. The level to which each of these factors has been studied is variable and for the most, far from complete.

Diel vertical migration of zooplankton, DVM, was first reported around 190 years ago (Cuvier, 1817) and represents the biggest migration, in terms of biomass, on the planet (Godlewska, 1996; Hays, 2003). DVM is believed to represent a classic trade-off between minimising predation risk and maximising food intake, with both predation risk and food intake decreasing with increasing depth (Alonzo and Mangel, 2001; Burrows and Tarling, 2004; Clark and Levy, 1988; De Robertis, 2002; Eiane and Parisi, 2001; Gabriel and Thomas, 1988; Iwasa, 1982). The classic pattern of DVM is such that zooplankton are in the upper food-rich waters at night, when predation risk is lower, and deep in food-poor waters during the day, when predation risk is high. However, the observed pattern of krill migration in the field is not always so straightforward, particularly in the region of South Georgia where the reverse pattern has been observed (Godlewska, 1996; Kalinowski, 1978). Such a converse observation highlights the importance of understanding the variability of conditions in a specific region, and how these affect the balance of a trade-off, in quantitative and qualitative terms.

At South Georgia during summer, both phytoplankton concentration and densities of the major land-based krill predators, fur seals, *Arcocephalus gazella*, and macaroni penguin, *Eudyptes chrysolophus*, are at their peak, which is higher than average for the Southern Ocean. Krill have a suite of predators other than seals and birds, including tactile nektonic predators such as chaetognaths and jellyfish (Hamner and Hamner, 2000; Hays, 2003), and pelagic fish (Barrera-Oro, 2002; Lancraft et al., 2004) that contribute an apparently consistent low level of predation throughout the year. In addition, these predators are present throughout most of the water column, on- and off-shelf, and can therefore be considered as a form of background mortality. Predation from land-based predators by contrast affects krill over a smaller spatial and temporal scale, and presents a risk that changes rapidly with depth, density and distance from land (Alonzo and Mangel, 2001; Hamner and Hamner, 2000; Lancraft et al., 2004; Perissinotto and McQuaid, 1992). The concentration of phytoplankton is highly variable around the Southern Ocean and particularly at South Georgia, where it is affected by bathymetry as well as seasonal and annual effects (Korb et al., 2004). Despite the fact that DVM has been studied intensively, often through the use of models (Eiane and Parisi, 2001; Tarling et al., 2000), there has been no effort to model the DVM of Antarctic krill in the South Georgia region, where variability in food and predation risk is high and the behavioural response complex. Nevertheless, the use of a simple behavioural model has the potential to explain complex behaviour.

Swarming or schooling affects the density of krill in the water column, which in turn affects the encounter rate with predators. It has long been established that krill form dense swarms, and that the size and density of swarms can modify the local environment (Mangel and Nicol, 2000; Marr, 1962). While many authors agree that a

variety of krill aggregations types are possible, and that understanding swarming is vital, there is little understanding of the underlying mechanisms (Burrows and Tarling, 2004; Miller et al., 1993). As with DVM, there are costs and benefits to swarming. Proposed benefits of swarming include reduced predation, through group avoidance strategies, and evasion and dilution factors once a predator attack is launched (O'Brien, 1987; Ritz, 2000). This would imply that krill would aggregate more densely in the presence of predators, for which there is some evidence (Zhou and Dorland, 2004), but see Hofmann et al. (2004). An additional benefit is reduced energy usage when in a school, from hydrodynamic advantages of swimming alongside neighbours, although there is little experimental evidence to support this (Ritz, 2000; Ritz et al., 2003). The primary cost of swarming is reduced ingestion due to intraspecific competition for food, although swarms also have the potential to find food over a greater range of distance (Hamner and Hamner, 2000; Morris et al., 1983; Ritz, 2000). Despite the fact that these costs and benefits are often quoted, there has been very little work into the relative importance of each. This is primarily due to the fact that it has been difficult to study because krill behave very differently in the laboratory than in the ocean, behaving more as individuals than as a school (Hofmann et al., 2004; Strand and Hamner, 1990; Swadling, 2005). The use of a model to represent the costs and benefits of swarming can therefore be very insightful in this instance, particularly when considering krill swarming behaviour in the context of a regional ecosystem.

Advection is explicitly identified in many modelling studies as a major factor in structuring marine ecosystems. This is particularly the case in the marine system at South Georgia where the input and loss of krill due to transport is thought to be important (Atkinson et al., 2001; Hofmann and Murphy, 2004; Loeb and Shulenberger,

1987). In addition, bathymetry is thought to be important because this helps relate the location of krill to the island, affecting predation risk as well as phytoplankton concentration. During summer, phytoplankton concentration is high in the waters around South Georgia, particularly at the shelf-break, with lower concentrations off-shelf, although this pattern is not always consistent (Korb et al., 2004). Predator densities from a central foraging place are highest close to the island and decrease exponentially with distance away (Houston and McNamara, 1985). At South Georgia, high concentrations of land-based predators are found on-shelf to the shelf-break (Barlow and Croxall, 2002a; Barlow and Croxall, 2002b; Hunt et al., 1992; Perissinotto and McQuaid, 1992). This situation presents a trade-off for krill, because areas with higher phytoplankton concentrations are also those with higher predator densities.

Krill are not passive particles, and there are a number of ways that they can respond to changing conditions. Firstly, by changing their depth and taking advantage of different current velocities at different depths, krill may be capable of changing or keeping their horizontal position (Hofmann and Murphy, 2004). There are examples of this type of behaviour in other animals, where DVM of copepods and the euphausiid *Meganycitiphanes norvegica* increased the probability of retention in an area of the Irish Sea (Emsley et al., 2005). Similarly there is the occurrence of selective tidal stream transport in the larvae and megalopa of the shore crab, *Carcinus maenus*, in Sweden and Portugal and the larval bay anchovy, *Anchoa mitchilli*, in Hudson River estuary, a process by which organisms move shallow or deeper in association with tidal movements to promote retention in shore (Queiroga, 1998; Queiroga et al., 2002; Rogers, 1940; Schultz et al., 2000). Secondly, krill are exceptionally strong swimmers (Hamner and Hamner, 2000), with maximum speeds up to 15 cm s^{-1} (Kils, 1981), which

is much faster than the currents immediately to the north of South Georgia, where the average maximum is only 3 cm s^{-1} for the month of January (Webb and de Cuevas, 1998; Webb and de Cuevas, 2003). Krill can adopt different types of swimming behaviour when searching or feeding, and these can increase or decrease the likelihood of staying in an area. There is some evidence that krill swim slower and turn more often in areas of high food concentration, swimming faster and turning less often in areas of low food concentration (Hofmann et al., 2004; McGehee and Jaffe, 1996; Price, 1989; Strand and Hamner, 1990); a phenomenon also observed in other animals (Bell, 1957; Hill et al., 2003). While a few studies have looked at the active transport of krill with currents (Fach et al., 2002; Hofmann and Lascara, 2000), there has been little work on the interaction between krill state, prevailing levels of food and predators, and advective forces.

In this chapter, a state-dependent dynamic programming model (SDP) is used to predict the occurrence of DVM, horizontal migration and swarming and its consequences on the distribution of krill close to South Georgia. SDP models have proven useful for understanding the trade-off between contrasting selective forces acting on decision making of consumers (Burrows et al., 2000; Houston et al., 1988; McNamara and Houston, 1986). In these models, optimal choices are predicted as a function of the state of the individual, which in this case relates to energy level and predation risk. Considering that krill at South Georgia face a number of contrasting conditions, and that a choice to move to a different depth or density of swarm can greatly affect both their likely energetic input and risk of predation, an SDP model is perfectly suited as a technique for predicting their short-term behaviour in the region.

AIM

The aim of this chapter is to create an SDP model for krill behaviour, specifically parameterised for the region of South Georgia. The output will show krill variability in behaviour in terms of depth, density of swarm and horizontal distribution. Krill in the model will respond to the variable conditions of phytoplankton availability, predator density, and currents, which will each change due to one or more factors including distance from island, depth and time of day.

METHODS

The model this chapter is based on is a state dynamic programming (SDP) model, used to predict the behavioural response of krill to changing conditions in an area of ocean to the north of Bird Island, South Georgia. Many parameters were required for the krill behaviour model, from krill respiration changing with krill size and swarm density to the concentration of phytoplankton changing with depth and position around South Georgia. The first section describes the parameterisation of the model, including the calculation of probabilities for krill changing zones each time step, depending on their swimming behaviour, using a simple particle movement program. This is followed by an explanation of the backward and forward iterations of the model, and a description of the runs of the model including the sensitivity analysis that assesses the robustness of predictions and relative strength of the tested parameter values.

The krill behaviour model

The krill behaviour model is a state dynamic programming model where krill respond to changing factors such as currents, distance from the island (South Georgia) and time of day. The krill behavioural response is measured in energy acquired over time, depth

choice, choice of swarm density, and type of swimming behaviour in terms of swim speed and turn rate. Each of the behavioural decisions affects how successful krill are in an area in terms of mortality and energy levels. In turn, the model is capable of predicting krill distribution around South Georgia and vertical migratory patterns, further affecting krill availability to predators in the region. Altering the parameterisation of the model gives an opportunity to examine how krill may respond to seasonal and interannual variability.

Setting up the krill swimming behaviour

Before designing the krill behaviour model, it was necessary to create a particle movement model in order to calculate the probabilities of individual krill changing zones, defined by latitude and longitude, each time step depending on their swimming behaviour. This was necessary because the swimming behaviour of krill was one of the state variables of the krill behaviour model of this chapter. A number of parameters were required for this initial model (

Table 3.1).

Table 3.1. List of parameters used to calculate the probability of krill changing zones, with unit, symbol and brief explanation.

Symbol	Parameter	Value	Unit
T	Time the model runs for	60	min
t	Time step	6	min
n	Number of individuals	10000	-
z	Zone: on-shelf, shelf-break, off-shelf	1,2 or 3	-
d	Depth: shallow or deep	1 or 2	-
Current(z,d)	Velocity of the current averaged over zone and depth	See Table 2	km h ⁻¹
s	Swimming speed of krill	0 to 0.54	km h ⁻¹
A	Direction of swimming, 90° is north	0 to 360	degrees

The particle movement model runs for a total of one hour, giving the result in terms of the probability of krill changing zones in that hour. The hour is divided into 10 time steps of 6 minutes (Table 3.1), where krill choose a swimming velocity and direction for each time step.

The area considered in the particle movement model, also describing the total area considered for the model in this chapter, is north of South Georgia, with Bird Island at the centre and bottom of the model region of interest (Figure 3.1). This location was chosen because krill predators dominate in the region, particularly macaroni penguins, *Eudyptes chrysolophus*, and Antarctic fur seals, *Arctocephalus gazella*. There are three zones in the model, defined as 1: onshore, 2: shelf-break and 3: offshore. These regions were chosen as biologically significant because they are known to differ in phytoplankton concentrations (Korb et al., 2004) current velocities (Atkinson et al., 2001; Brandon et al., 2000), and predator concentrations (Hunt et al., 1992). The latitudinal boundaries for the three zones were based on bathymetric maps of South Georgia, in which the shelf-break was between 500 m to 2000 m depth.

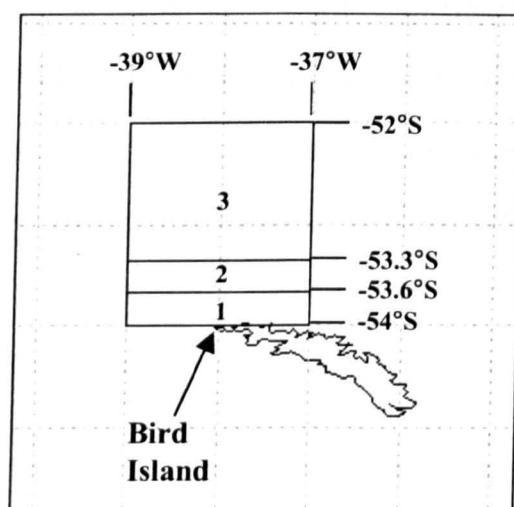
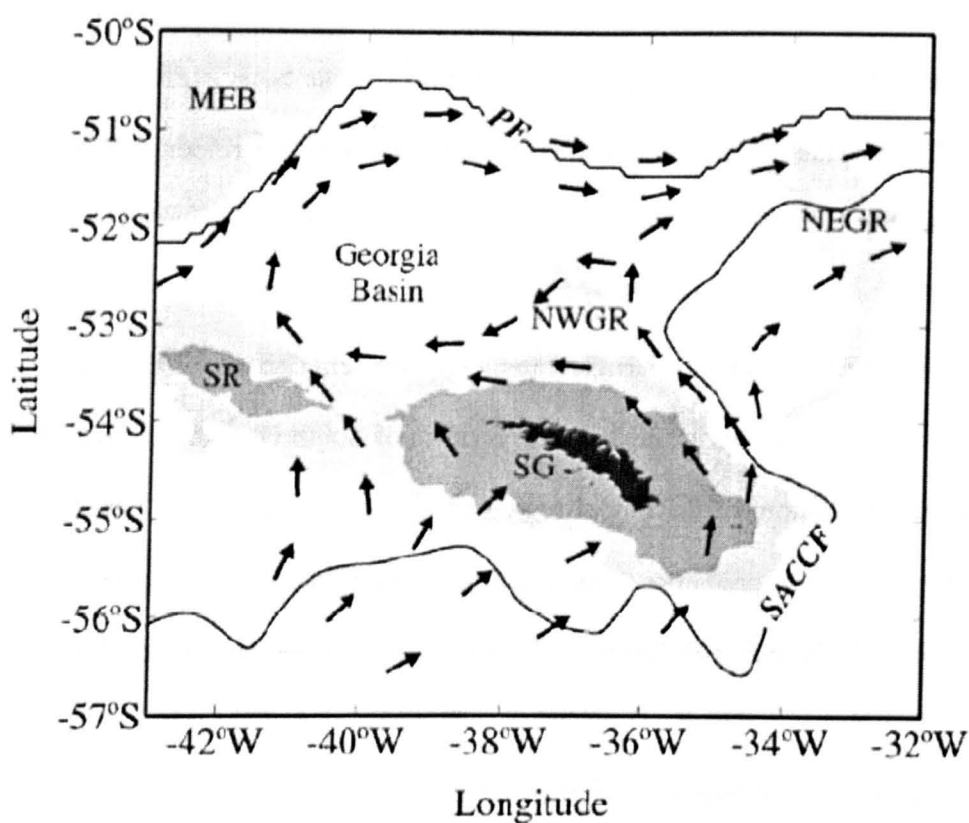


Figure 3.1. Map above shows South Georgia with general flow patterns, where dark grey areas signify depths of 500m or less and light grey areas 2500m or less (Korb et al., 2004; Trathan et al., 1997). Map below shows the area represented in the model, showing Bird Island at the North western tip, with the model zones defined as 1: onshore, 2: shelf-break and 3: offshore, and their boundary latitude and longitude positions.

There are two depth zones in the model, defined as shallow <60 m and deep 60-150 m. The depth of vertical migration for krill is most likely associated with the diving depths of predators during the day (Zhou and Dorland, 2004). Therefore, depths were chosen based on the average dive range of the main land-based predators at Bird Island, shallow water being in the range of most diving predators, and deep water predominantly out of this range. Macaroni penguins dive to an average of 35m in the day (Croxall et al., 1993), with occasional longer dives from 40 to 50m (Green et al., 2003). Antarctic fur seals can dive 50 to 80m in the daytime, although ~60% of dives are <20m (Boyd and Croxall, 1992). Visibility also decreases rapidly with depth, making the depth division biologically significant to krill in terms of likely mortality.

Once the water column was divided, characteristic current velocities for each depth interval were determined using the modelled velocity output from the Ocean Circulation and Climate Advanced Modelling (OCCAM) Project model (Webb and de Cuevas, 1998; Webb and de Cuevas, 2003). OCCAM is a global numerical ocean circulation model with a horizontal resolution of 1/4 degree by 1/4 degree and 36 vertical levels, forced with time-varying wind fields. Monthly mean velocities for January 1997 to 2000 were depth weight-averaged to give horizontal velocity data for the upper 64 m of the water column and the lower 64-147 m (by averaging OCCAM levels 1-3 and 4-6 respectively), which were closest to the 2 chosen depth intervals. For each zone, an average current velocity was calculated, which was further averaged across all five years of data (Table 3.2).

Table 3.2. Current velocity km h^{-1} , divided into eastward and northward components, for each depth and zone.

Zone	Shallow (0-64 m)		Deep (>64 m)	
	Eastward	Northward	Eastward	Northward
1 – on-shelf	-0.00696159	0.063953	-0.027	0.008738
2 – shelf-break	-0.099051978	0.074367	-0.1102	0.019774
3 – off-shelf	0.034928133	0.096697	0.018488	0.032565

The swimming speed of krill is mainly within the range of 0 to 15 cm s^{-1} (Kils, 1981), which converts to 0 to 0.54 km h^{-1} . Krill expend an equal amount of energy at any horizontal swimming speed $< 15 \text{ cm s}^{-1}$, because they change speed by simply changing the vertical position of their body in the water (Kils, 1981). The swimming speed of krill in combination with angle of turn, altering horizontal direction from one time step to the next, may be important in determining whether a krill is more likely to be retained in or dispersed from a given area. The angle A signifies their horizontal angle of turn relative to the direction they were facing at the previous step, with A having a different range for each of the 3 models. Firstly described is a situation where the krill swims randomly, with speed and angle of turn randomly chosen at each time step during the hour (Figure 3.2).

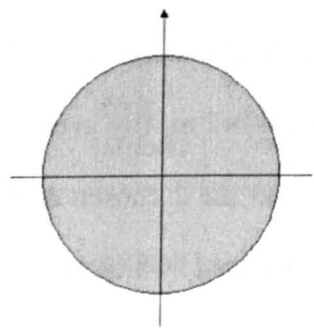


Figure 3.2. Random swim behaviour. New direction is randomly chosen out of the entire 360° range. Speed of new vector is randomly chosen between 0 and the maximum of 0.54 km h^{-1} .

There is evidence that krill slow their swimming speed and turn more often in favourable areas, such as areas of high food concentration (McGehee and Jaffe, 1996; Strand and Hamner, 1990), which is also a widespread phenomenon in other species (Bell, 1957; Hill et al., 2003; Price, 1989). Therefore, in the second model, the new angle of turn relative to the direction in the previous time step is an angle randomly chosen between 135° and 225° ; a high angle of turn (Figure 3.3). For swimming speed, the program generates a random number between 0 km h^{-1} and half the maximum speed, 0.27 km h^{-1} , to simulate a slow swimming speed.

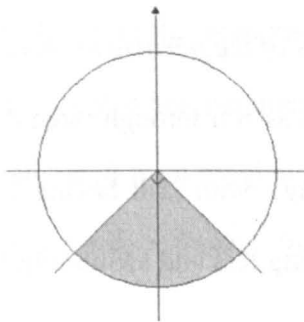


Figure 3.3. Swimming behaviour to stay in same area. Arrow shows the direction of swimming in the previous time step, with new direction chosen randomly from the shaded area 45° to each side opposite of the initial direction. Speed of the new vector is randomly chosen from the lower half of the swim speed range.

The third option represents a situation where krill have the opportunity to disperse from an area, based on evidence that swimming animals display a faster swimming speed and lower rate of turn in unfavourable areas (McGehee and Jaffe, 1996; Price, 1989). In this model, the program randomly generates an angle of turn between 0 and 45° each side of the direction in the previous time step, representing a low angle of turn. Simulated krill randomly choose a fast swimming speed; in the top half of the swimming speed range (Figure 3.4).

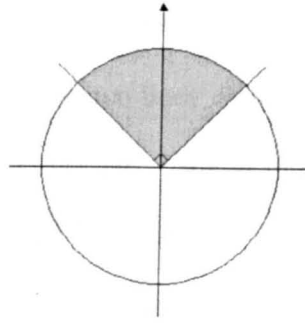


Figure 3.4 Disperse swim behaviour. Arrow shows the direction of swimming in the previous time step, with new direction chosen randomly from the shaded area 45° to each side of the initial direction.

Workings of the particle movement model

The particle movement model was run through three different scenarios: A (Random): with random movement, B (Stay): with krill having a sharper turn and slower speed, and C (Disperse): with krill turning less and swimming faster.

In each simulation of the model, individual krill were seeded randomly onto the landscape, placing each individual in zone 1, 2 or 3 (Figure 3.1). The initial latitude and longitude were recorded, and the krill had a chance to move across the landscape according to the rules of the model (Equation 1, Equation 2, Equation 3). This occurred through a series of ten 6-minute time steps. The model recorded whether the individual moved out of the zone by the end of the hour, distinguishing movement into another zone from movement out of bounds. This was repeated for $n = 1000$ individuals to give a proportion of krill in zone x moving to zone y in one hour, with the entire process repeated 100 times to give an average probability.

Equation 1	Model A (Random): $A(t) = Rnd \cdot 360$
Equation 2	Model B (Stay): $A(t) = A(t - 1) + 180 \pm Rnd \cdot 45$
Equation 3	Model C (Disperse): $A(t) = A(t - 1) \pm Rnd \cdot 45$

Where $A(t)$ is the angle of turn at time t . Results of the particle movement model are shown in the following section.

Parameters of the krill behaviour model

Aside from setting up the likely effects of the state parameter swimming behaviour on krill distribution and advection, many other parameters were required for the krill behaviour model. These were estimated from previous studies and available data, with this section describing the most accurate estimates for each of the parameters (Table 3.3).

Table 3.3. List of parameters used in the model.

Symbol	Parameter	Value	Unit
$F(e,z,m,t)$	Fitness is based on krill energy state and zone and changes for small and large krill with time	0 to 200	-
$F(T)$	Terminal fitness reward	0 to 200	-
i	Behavioural decisions made by individual krill at each time step	1 to 18	-
n	Number of individuals	10 000	-
T	Final time step	1500	h
t	Time step	1	h
L	Time of day	1 day or 2 night	-
d	Krill depth	1 shallow or 2 deep	-
s	Swarm density, low to high	1 to 3 (see table)	-
a	Choice of swimming turn rate and swim speed affecting advection	1 to 3 (see table)	-
z	Zone, relative to the continental shelf	1 to 3 (see table)	-
e	Energy level	0 to 200	mg C
m	Total length (TL) of individual krill	small 30, large 50	mm
$WW(m)$	Wet weight, based on TL	small 209, large 1046	mg
$DW(m)$	Dry weight, based on TL	small 45, large 226	mg
$CW(m)$	Carbon weight, based on TL	small 19, large 101	
$Phyt(d,z)$	Concentration of phytoplankton in the water, depends on depth and zone	$0.04 < Phyt < 3.2$	mg C m ⁻³
$Filt(DW)$	Filtration rate of phytoplankton depends on DW	small 0.001, large 0.002	mg C h ⁻¹
$Ffactor(s)$	Filtration reduced by factor with krill density	0.1 to 1	-
X	Assimilated ingested energy	$3e-6 < X < 0.005$	mg C h ⁻¹
$Resp(m,s)$	Respiration depends on krill size and swarm density	$0.01 < Resp < 0.05$	mg C h ⁻¹
$Rdensity(s)$	Respiration decreases by factor with density	0 to 0.2	-
$Rfactor(ing)$	Respiration increases by factor with ingestion	1 to 2	-
$Mort(t,d,s,z)$	Mortality risk depends on time of day, depth, swarm density and zone	$2.5e-8 < Mort < 0.285$	Probability h ⁻¹
$Pzone(d,a,z,y)$	Probability of moving between zones depends on depth, swim speed and turn rate, current zone z and new zone y	$0 < Pzone < 0.999666$	Probability h ⁻¹

The fitness function, F , in the model was linearly related to the energy state of the krill and was affected by the risk of mortality. Fitness increased with assimilated energy from ingestion and decreased with respiration. Each time step, the model krill attempted to maximise fitness by maximising ingestion, minimising respiration costs and considering the risk of mortality.

The terminal reward function, $F(T)$, defines the fitness reward at the final time T , dependent on the krill reaching a target energy level; different in this case for small and large krill. The target level was based on observed growth rates of small and large krill during summer in the South Georgia region, with a growth rate of approximately 0.2 mm d⁻¹ for small krill and 0.1mm d⁻¹ for large krill converted to units of mg C day⁻¹ (Tarling et al., 2006). Based on a small krill size of 30mm and large krill of 50mm, and converting krill length into carbon weight (Hofmann and Lascara, 2000), this translates that small krill would need to ingest 2.7% of their body weight per day, and large krill 1.6% of their body weight per day at this time of year to reach target growth rates. The energy level required for a fitness reward r_m is the amount of assimilated carbon (ingestion minus respiration) that the krill would need in order to achieve the specified growth rate. If the krill did not acquire the required amount of energy by the final time T there was no fitness reward, otherwise fitness was equal to the total amount of carbon assimilated by time T .

Equation 3-4

$$F(T) = \begin{cases} 0 & ; \quad e < r_m \\ e & ; \quad e \geq r_m \end{cases}$$

where r_m is the required energy level, based on krill size, m , for a fitness reward at the final time T , and e is the total assimilated carbon.

$$\text{Equation 3-5} \quad r_m = \begin{cases} CW_m \cdot T / 24 \cdot 0.0067 & ; \quad m = 30 \\ CW_m \cdot T / 24 \cdot 0.002 & ; \quad m = 50 \end{cases}$$

where CW_m is carbon weight of krill depending on m , 0.0067 and 0.002 are the respective proportions of carbon weight that small and large krill must end up with at the end of each day to reach target growth rates at South Georgia in January (Tarling et al., 2006).

The model ran for a total of 1500 hours, approximately 2 months. However, results were taken from the middle month, from 376 to 1125 hours, to minimise artefacts that are inherent in this type of model where the terminal reward function would signify death of the individual. In an SDP model, behaviour changes as time t approaches the final time T because there is little time remaining and the organism must pick either the risky patch or the safe patch (Mangel and Clark, 1988). As the remaining time increases, the behavioural decisions become relatively insensitive to the value of t and depend more on the state variables (Mangel and Clark, 1988). This is known as stationarity (Mangel and Clark, 1988). Taking the middle section of time from the model results is useful because it simplifies their interpretation (Clark and Mangel, 2000; Mangel and Clark, 1988).

For the current model, the parameters estimations were based on the month of January, when penguins and seals are constrained to land for the breeding season (Barlow et al., 2002; Barlow and Croxall, 2002b; Green et al., 2002; Williams and Croxall, 1991). The time step of the model was one hour, based on the assumption that krill make major behavioural decisions, to migrate or feed, at scales in the order of hours and even days, rather than minutes and seconds. This is reasonable when considering krill behaviours such as diel vertical migratory behaviour and considering that the model runs for one month and decisions such as change of depth and advection into other zones would happen over a time scale greater than minutes or seconds (but see Tarling and Johnson (2006)).

Swarm density refers to the three dimensional density of a krill swarm, krill m^{-3} . Various classifications have been made on the biological composition of swarms, with divisions such as feeding, searching, breeding and moulting swarms of varying size and density (Ricketts et al., 1992), although this model does not consider breeding or moulting. Krill in the model chose a swarm density based on: the benefits of increased swarm density, including protection from predation (Burrows and Tarling, 2004; Hamner and Hamner, 2000; Ritz, 1994) and possible energetic savings (Ritz, 2000); and the costs of increased swarm density, in terms of reduced ingestion (Antezana and Ray, 1984; Burrows and Tarling, 2004; Hamner and Hamner, 2000; Ritz, 2000). Swarm classifications were based on those observed and estimated in the field (Hamner and Hamner, 2000), classified as low, medium and high density swarms (Table 3.4).

Table 3.4. Swarm density classification.

Density (s)	Krill m ⁻³
1 – low	< 100
2 – medium	100 – 1000
3 – high	> 1000

There were 3 zones, *z*, in the model, divided in terms of bathymetry as an on-shelf, shelf-break and off-shelf zones (Table 3.5, but see also Figure 3.1).

Table 3.5. Zone classification

Zone (<i>z</i>)	Relative to shelf
1	On-shelf
2	Shelf-break
3	Off-shelf

Krill had a choice of three types of swimming behaviour each time step, affecting the probability of dispersing from or being retained in a particular zone (Table 3.6). These behaviours are described fully in the following section.

Table 3.6. Choice of swimming behaviour each time step.

Swimming behaviour (<i>A</i>)	Swim speed Turn rate	
	Swim speed	Turn rate
1 – Random	Random	Random
2 – Stay	Low	High
3 – disperse	High	Low

The probability of an individual krill moving from zone z to zone y in one time step $P_{zone}(d,a,z,y)$, calculated previously by the particle movement model, was based on d , a , z , and y . There were separate probabilities for the model A (Random), with random swimming and speed (Table 3.7), model B (Stay), with slow swimming speed and high turn rate (Table 3.8), and model C (Disperse), with high swimming speed and low turning rate (Table 3.9).

Table 3.7. Probability of an individual changing zones in one time step in model Random, with random swimming speed and turn rate, in shallow water

Depth	To				
	From	Zone 1	Zone 2	Zone 3	Out of bounds
Shallow	Zone 1	0.998249505	0.001536634	0	0.000213861
	Zone 2	0.000134653	0.997145545	0.002343	0.000377228
	Zone 3	0	1.78218E-05	0.999104	0.000878218
Deep	Zone 1	0.999039604	0.000724752	0	0.000235644
	Zone 2	0.000593069	0.997864356	0.001134	0.000408911
	Zone 3	0	8.51485E-05	0.999366	0.000548515

Table 3.8. Probability of an individual changing zones in one time step in model Stay, with slow swimming speed and high turn rate, in shallow and deep water.

Depth	To				
	From	Zone 1	Zone 2	Zone 3	Out of bounds
Shallow	Zone 1	0.998493069	0.001448515	0	5.84158E-05
	Zone 2	0	0.99739802	0.002234	0.000368317
	Zone 3	0	0	0.999236	0.000764356
Deep	Zone 1	0.99959802	0.00030099	0	0.00010099
	Zone 2	3.46535E-05	0.998932673	0.000654	0.000378218
	Zone 3	0	9.90099E-07	0.999666	0.000332673

Table 3.9. Probability of an individual changing zones in one time step in model Disperse, with high swimming speed and low turn rate, in both shallow and deep water.

Depth	To				
	From	Zone 1	Zone 2	Zone 3	Out of bounds
Shallow	Zone 1	0.996056436	0.00320297	0	0.000740594
	Zone 2	0.002292079	0.99250099	0.004395	0.000811881
	Zone 3	0	0.000430693	0.997693	0.001876238
Deep	Zone 1	0.996681188	0.002529703	0	0.000789109
	Zone 2	0.002972277	0.992621782	0.003595	0.000810891
	Zone 3	0	0.000656436	0.997697	0.001646535

Energy level, *e*, was calculated in mg C, which is the common unit for many krill energetic models (Fach et al., 2002; Hofmann and Lascara, 2000). In the model, energy was not converted into growth, but represented the accumulated assimilated energy over time. It is difficult to convert energy into growth in a model, because the interaction between temperature, food and growth rates is complex (Fach et al., 2002).

Krill size, *m*, was considered as small, 30mm, and large, 50mm, representing the mean values for krill sizes at South Georgia in January (Tarling *et al.* In Press). Sex of the krill was not considered.

The conversions between wet, dry and carbon weights were taken from Hofmann and Lascara (2000) (Table 3.10).

Table 3.10. Conversions, where WW is wet weight (mg), DW is dry weight (mg), L is length (mm), and CW is carbon weight (mg C).

Size (mm)	Equation	Units
< 40	$WW = 0.0072 \cdot L^{3.021}$	mm to mg C
> 40	$WW = 0.0016 \cdot L^{3.423}$	mm to mg C
-	$DW = 0.216 \cdot WW$	mg to mg C
-	$CW = 0.366 \cdot DW^{1.037}$	mg to mg C

Phytoplankton concentrations, $Phyt(d,z)$, were estimated from SeaWiFS data averaged over the month of January from 2000 to 2004 for each zone in the simulated area (Table 3.11). These values are shown in mg chlorophyll m^{-3} but were later converted to mg C through multiplying by 50 (Atkinson, 1996). Average phytoplankton was much higher in 2000 compared to 2004 so these 2 years were used as examples of high and low phytoplankton scenarios (Table 3.11). The ratio of phytoplankton concentration between the zones, i.e. on-shelf to the shelf-break, shelf-break to off-shelf, were relatively similar in 2000 and 2004 with no anomalous high or low values as seen in 2002 (Table 3.11).

The relationship between chlorophyll in the surface waters and chlorophyll at depth was determined by examining chlorophyll depth profiles from *in situ* measurements from a number of surveys on the RRS *James Clark Ross* (Rebecca Korb, unpublished data, British Antarctic Survey) (Figure 3.5).

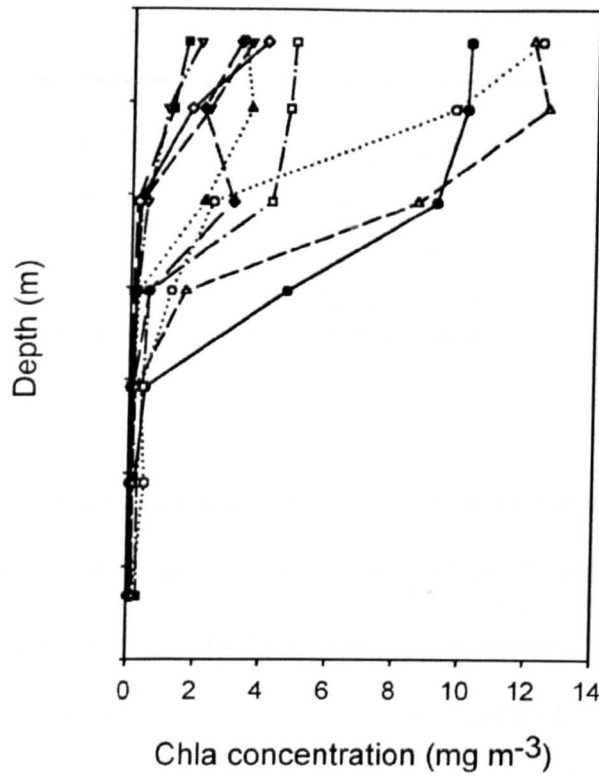


Figure 3.5. Chlorophyll depth profiles from *in situ* measurements from the RRS *James Clark Ross* (Rebecca Korb, unpublished data, British Antarctic Survey) from a range of sites to the northwest of South Georgia (-37 to -38° W; -53.5 to -53° S).

The change in chlorophyll concentration with depth was calculated by dividing concentration in the shallow ($<60\text{m}$) and by that in the deep ($>60\text{m}$). On average, deep-water concentration was 20x lower than shallow water, so the SeaWiFS shallow values were divided by 20 to give deep concentrations of phytoplankton in the deep water for each of the zones (Table 3.12).

Table 3.11. Average SHALLOW concentration (\pm standard error) of phytoplankton for the month of January, mg chlorophyll m⁻³, for each year and averaged over each zone. Highlighted are values for the year 2000, average high levels, and 2004, low levels of phytoplankton.

Zone	Year				
	2000	2001	2002	2003	2004
On-shelf	2.1 \pm 0.115	0.6 \pm 0.022	1.8 \pm 0.103	1.8 \pm 0.126	1.7 \pm 0.152
Shelf-break	3.2 \pm 0.103	0.4 \pm 0.023	4 \pm 0.101	3.5 \pm 0.126	1.6 \pm 0.152
Off-shelf	1.4 \pm 0.103	0.5 \pm 0.023	6 \pm 0.102	2.7 \pm 0.125	0.8 \pm 0.152

Table 3.12. Average DEEP concentration of phytoplankton for the month of January, mg chlorophyll m⁻³, calculated by dividing shallow values by 20. Highlighted are values for the year 2000, average high levels, and 2004, low levels of phytoplankton.

Zone	Year				
	2000	2001	2002	2003	2004
On-shelf	0.105	0.03	0.09	0.09	0.085
Shelf-break	0.16	0.02	0.2	0.175	0.08
Off-shelf	0.07	0.025	0.3	0.135	0.04

The filtration rate for individual krill was measured in mg C h⁻¹ (Hofmann and Lascara, 2000).

Equation 3-6

$$Filtration_{s,m} = (0.00343 \cdot DW^{0.514}) / 24 \text{ (mg C h}^{-1}\text{)}$$

Filtration rate in the model also depended on density of swarm, such that the rate decreased as density increased (Morris et al., 1983; Ritz, 2000). It is to be noted that there is presently very little experimental evidence of the effect of swarm density on filtration rate, with only one study giving actual values (Morris et al., 1983).

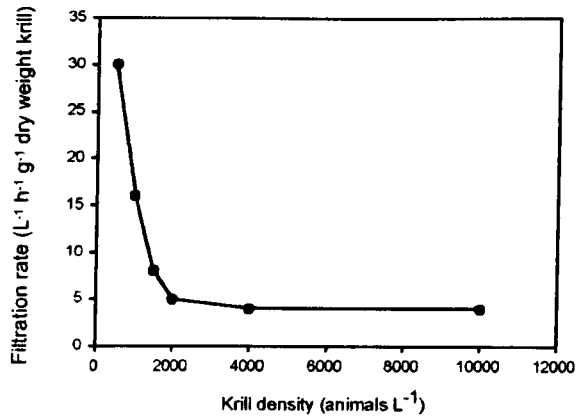


Figure 3.6. Approximated relationship between filtration rate and krill density for adolescent krill (Morris et al., 1983).

The scaling for filtration with increasing krill density was approximated, assuming that there was no reduction in filtration for krill densities of <100 (*Ffactor* = 1; Table 3.13).

Table 3.13. Filtration rate was multiplied by a filtration factor, *Ffactor*, that was directly estimated from the above figure (Morris et al., 1983).

Swarm density (krill m ⁻³)	<i>Ffactor</i>
1: < 100	1
2: 100 - 1000	0.5
3: > 1000	0.1

This factor was multiplied by the filtration rate.

Equation 7

$$Filtration_{s,m} = \left[(0.00343 \cdot DW^{0.514}) / 24 \right] Ffactor \text{ (mg C h}^{-1}\text{)}$$

Ingestion X was calculated by multiplying filtration rate by phytoplankton concentration in mg C m^{-3} , and scaling down by an assimilation rate of 0.8 (Clarke and Morris, 1983; Fach et al., 2002; Hofmann and Lascara, 2000; Ikeda, 1983).

Equation 3-8
$$X = \text{Filtration}_{s,m} \cdot \text{Phyt}_{d,z} \cdot 0.8$$

where $\text{Phyt}_{d,z}$ is in mg C m^{-3} using a factor of 50 to convert from $\text{mg chlorophyll m}^{-3}$ (Atkinson, 1996).

The total respiration cost for each size class was calculated as standard metabolism, R , plus an increase due to feeding (Hofmann and Lascara, 2000) and a decrease with increasing swarm density.

Firstly, respiration decreased with increasing swarm density

Equation 3-9
$$R = \frac{(0.847 \cdot DW^{0.85})}{1000} \cdot R_c \cdot R_{\text{density}_s}$$

where R_c is the conversion factor, to convert mL O_2 to mg C , set at 0.5357 from the comparison of many different studies on oxygen uptake in sub adult and adult krill (Hofmann and Lascara, 2000). R_{density_s} was based on a study where mysids in aggregations consumed less oxygen per weight than non-aggregating individuals due to proposed hydrodynamic advantages of swimming alongside neighbours (Ritz, 2000). Other evidence came from an experiment on 14 species of fish, where individual fish separated from their school mates consumed oxygen at around twice the rate of school

members (Parker, 1975). There is no experimental work on krill because no-one has yet managed to make them school in the laboratory (Hofmann et al., 2004; Strand and Hamner, 1990; Swadling, 2005). There is evidence that feeding krill can use up to twice the amount of oxygen than non-feeding krill (Hofmann and Lascara, 2000; Ritz, 2000), however this figure would only be relevant if the non-feeding krill were swarming. Therefore, a reduction in respiration due to increased swarm density was estimated from studies on other organisms (Table 3.14).

Table 3.14. Respiration was multiplied by *Rdensity* representing the decrease in respiration with increasing swarm density.

Swarm density (krill m ⁻³)	Rdensity
1: < 100	1
2: 100 – 1000	0.9
3: > 1000	0.8

In addition, respiration increases with ingested food

Equation 3-10

$$R = R \cdot (1 + R_f)$$

where *R* is standard metabolism, and *R_f* the feeding activity factor (Hofmann and Lascara, 2000). *R_f* increases linearly from 0 to 1 for a % daily ration (mg C) of 0 to 10 % (Figure 3.7).

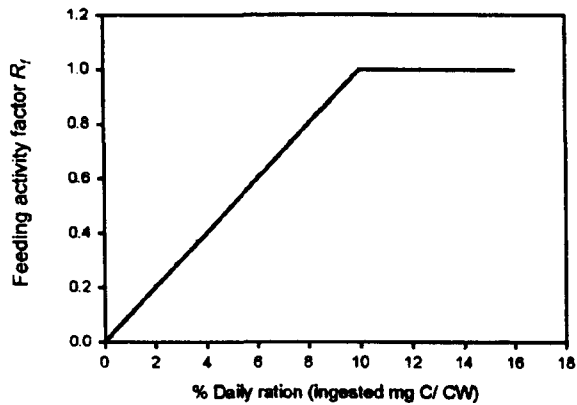


Figure 3.7. Feeding activity factor, R_f , as a function of % daily ration, calculated as ingestion/body weight (Hofmann and Lascara, 2000)

Mortality in the model, $Mort(t,d,s,z)$, signified a risk of death for an individual per time step. There were 4 components that affected mortality, time of day (t), depth (d), density of swarm (s), and zone (z). A log-odds ratio technique was used to place differing mortality probabilities around the mean value. Log-odds ratios form the basis of most statistical models dealing with the likelihood of particular outcomes. The most familiar examples are in medicine where the outcomes are life or death after a particular time has elapsed. The effects of different treatments (drugs, placebos etc) are compared among groups by their effect on the log odds ratio of surviving or getting better.

The distance of krill from shore could affect their likelihood of mortality where there was a significant contribution to mortality from land-based predator colonies, as at South Georgia (Atkinson et al., 2001; Barlow and Croxall, 2002b; Murphy et al., 1998; Trathan et al., 1998). The mortality at the shelf-break was based on the average mortality for krill close to an island, decreasing by half off-shelf where predator density was lower, and increasing twofold on-shelf where predator densities were higher (Table

3.15). Previous studies on both fur seals and macaroni penguins during summer at Bird Island, South Georgia, show a decrease in density with increasing distance from the island (Hunt et al., 1992; Perissinotto and McQuaid, 1992). This was attributed to central place foraging theory, considering both species forage from a central place at this time of year, so there would be an expected dilution of numbers with increasing area, in addition to the energetic constraint of foraging to a certain distance from shore (Houston and McNamara, 1985; Hunt et al., 1992). This is an example of how the log-odds ratio is weighted around an average mortality. Looking at the results from this paper, it is reasonable to assume that the difference in total predator density on-shelf to off-shelf is in the order of $10^{0.6}$ as opposed to 10^1 or more (Hunt et al., 1992). The importance of this estimation to final results was investigated in the sensitivity analysis.

In order to use the log-odds ratio, it was necessary to define an estimate of how each factor could increase or decrease mortality from the average (Table 3.15). The total difference in mortality between day and night, shallow and deep was estimated on an optimisation model of DVM of northern krill in the Clyde Sea, with predominantly visual pelagic fish predators (Tarling et al., 2000). Macaroni penguins would have a similar relative effect on the different mortalities associated with krill habitat choice because they are also visual predators, diving predominantly in daylight in January, with some dives at night meaning there is still risk for krill at this time (Croxall et al., 1993; Green et al., 2003).

Table 3.15. Mortality was affected by 10^y ; each of these components was considered in the mortality function.

Component	y
Day shallow	+ 3
Day deep	- 1
Night shallow	- 3
Night deep	+ 1
Swarm density 1	+ 0.3
Swarm density 2	0
Swarm density 3	- 0.3
On-shelf	+ 0.3
Shelf-break	0
Off-shelf	- 0.3

The maximum difference in mortality between a low-density swarm and a high-density swarm was estimated at $10^{0.6}$, approximately a factor of 4 (Table 3.15). The proposed benefits of swarming, in reducing mortality, include increased vigilance and group avoidance strategies, and evasion and dilution factors once an attack is launched (Ritz, 2000). These strategies are effective against visual predators that predate krill individually, such as those predators based at Bird Island, South Georgia during summer. Unfortunately, there is no quantitative data on how swarming reduces mortality, so an estimation was made in relation to other factors affecting mortality. This parameter was tested in the sensitivity analysis.

There was an average mortality of krill, where

Equation 3-11

$$Mortality = 1 - e^{-\beta \cdot I}$$

There are different estimations of β for the above equation, where the time step t is 1 year, from $\beta = 1.9$ (Reid et al., 2002; Siegel, 2000b) to 1 (Burrows and Tarling, 2004). Using $\beta = 1$ gives a survival for one year of ~3680 krill from 10 000, which when divided into a time step of 8760 lots of 1 hour, gives a $\beta = 0.0001$ for one hour. This was used as the β to calculate the average mortality in the model.

Now, to find the logit (l)

Equation 3-12
$$l = \log_{10} \left[\frac{P}{(1-P)} \right] = \log_{10} \left[\frac{0.0001}{(1-0.0001)} \right] = -4$$

For each combination of depth, density, time and zone, values of y (Table 3.15) were added together to make x . For example, if a krill was in a shallow, low-density swarm in zone 1 at night, $x = 2 + 1 + 1 - 1 = 3$ this value is represented in (Table 3.16).

The next step was to find x' such that

Equation 3-13
$$x' = l + x$$

and finally, the new probability of mortality with this combination of factors, time of day etc, affecting mortality

Equation 3-14
$$P' = \frac{10^{x'}}{(1+10^{x'})}$$

Table 3.16. Mortality probabilities, P' , for all the different combinations of depth (d), density (s), time of day (time) and zone (z), in probability of mortality h^{-1} . The second last two columns estimate how many krill would remain after a specified time interval, from an original number of 1 000 000, and the last column is the β value for mortality with a time step of 1 year.

d	s	time	z	x	x'	P'	Survive h	Survive yr	β yr
Shallow	1	Day	1	3.6	-0.4	0.334	666 139	0	-
Shallow	1	Day	2	3.3	-0.7	0.201	799 239	0	-
Shallow	1	Day	3	3	-1	0.112	888 184	0	-
Shallow	1	Night	1	1.6	-2.4	0.005	995 013	9.55E-14	43.794
Shallow	1	Night	2	1.3	-2.7	0.003	997 494	0.000285	21.976
Shallow	1	Night	3	1	-3	0.001	998 742	16	11.042
Shallow	2	Day	1	3.3	-0.7	0.201	799 239	0	-
Shallow	2	Day	2	3	-1	0.112	888 184	0	-
Shallow	2	Day	3	2.7	-1.3	0.059	940 649	1.6E-227	535.98
Shallow	2	Night	1	1.3	-2.7	0.003	997 494	0.000285	21.976
Shallow	2	Night	2	1	-3	0.001	998 742	16	11.042
Shallow	2	Night	3	0.7	-3.3	0.001	999 369	3984	5.5255
Shallow	3	Day	1	3	-1	0.112	888 184	0	-
Shallow	3	Day	2	2.7	-1.3	0.059	940 649	1.6E-227	535.98
Shallow	3	Day	3	2.4	-1.6	0.031	969 346	3.6E-113	272.72
Shallow	3	Night	1	1	-3	0.001	998 742	16	11.042
Shallow	3	Night	2	0.7	-3.3	0.001	999 369	3984	5.5255
Shallow	3	Night	3	0.4	-3.6	0	999 683	62 679	2.7697
Deep	1	Day	1	-0.4	-4.4	0	999 949	644 662	0.439
Deep	1	Day	2	-0.7	-4.7	0	999 974	802 487	0.22
Deep	1	Day	3	-1	-5	0	999 987	895 582	0.1103
Deep	1	Night	1	-2.4	-6.4	0	999 999	995 619	0.0044
Deep	1	Night	2	-2.7	-6.7	0	999 999	997 802	0.0022
Deep	1	Night	3	-3	-7	0	999 999	998 897	0.0011
Deep	2	Day	1	-0.7	-4.7	0	999 974	802 487	0.22
Deep	2	Day	2	-1	-5	0	999 987	895 582	0.1103
Deep	2	Day	3	-1.3	-5.3	0	999 993	946 228	0.0553
Deep	2	Night	1	-2.7	-6.7	0	999 999	997 802	0.0022
Deep	2	Night	2	-3	-7	0	999 999	998 897	0.0011
Deep	2	Night	3	-3.3	-7.3	0	999 999	999 447	0.0006
Deep	3	Day	1	-1	-5	0	999 987	895 582	0.1103
Deep	3	Day	2	-1.3	-5.3	0	999 993	946 228	0.0553
Deep	3	Day	3	-1.6	-5.6	0	999 996	972 678	0.0277
Deep	3	Night	1	-3	-7	0	999 999	998 897	0.0011
Deep	3	Night	2	-3.3	-7.3	0	999 999	999 447	0.0006
Deep	3	Night	3	-3.6	-7.6	0	999 999	999 723	0.0003

Running the model

The individual chooses from one of 18 decisions each time step, with a choice of each 1: swimming speed and turn rate, 2: depth and 3: swarm density (Table 3.17). For example, krill choosing decision 1 would swim with a random swim speed and turn

rate, at a shallow depth, in a medium density swarm for one time step. Each of these decisions has costs and benefits in terms of total mortality and energy intake.

Table 3.17. All the behavioural decisions, i , of krill in the model.

i	Swim behaviour (a)	Depth (d)	Swarm density (s)
1	Random	Shallow	Low
2	Random	Shallow	Medium
3	Random	Shallow	High
4	Random	Deep	Low
5	Random	Deep	Medium
6	Random	Deep	High
7	Stay	Shallow	Low
8	Stay	Shallow	Medium
9	Stay	Shallow	High
10	Stay	Deep	Low
11	Stay	Deep	Medium
12	Stay	Deep	High
13	Disperse	Shallow	Low
14	Disperse	Shallow	Medium
15	Disperse	Shallow	High
16	Disperse	Deep	Low
17	Disperse	Deep	Medium
18	Disperse	Deep	High

Backward iteration

The decision, i , chosen at time t is that which maximises the fitness, F , at time $t + 1$, calculated from the resulting assimilated energy, minus respiration, from each decision i and also considering the risk of mortality, β_i , with each. The fitness function also differs for krill of a different size m .

Equation 3-15
$$F(e, m, t) = \max_i (1 - \beta_i) F(e'_i, m, t + 1)$$

Further, fitness is affected at the end of each time step by the probability of krill changing zones, which is determined by krill swimming behaviour a and krill depth d .

This gives the resulting fitness function used in the model when krill has the opportunity of moving from the current zone z to new zone y .

Equation 3-16
$$F(e, m, z, t) = \max_i \sum_{y=1}^3 P_{zone}(d'_i, a'_i, z, y) \cdot (1 - \beta_i) \cdot F(e'_i, m, y, t + 1)$$

So krill eats and survives at the start of the time step, and chooses i to maximise energy intake and minimise mortality. In addition, there is an expected effect of swim behaviour a on advection and the consequences of this decision for future ingestion, costs and survival.

Energy at time $t+1$ is calculated by energy at time t plus assimilated energy from ingestion minus the cost of respiration resulting from decision i (Figure 3.8).

Equation 3-17
$$e' = e + X_i - resp_i$$

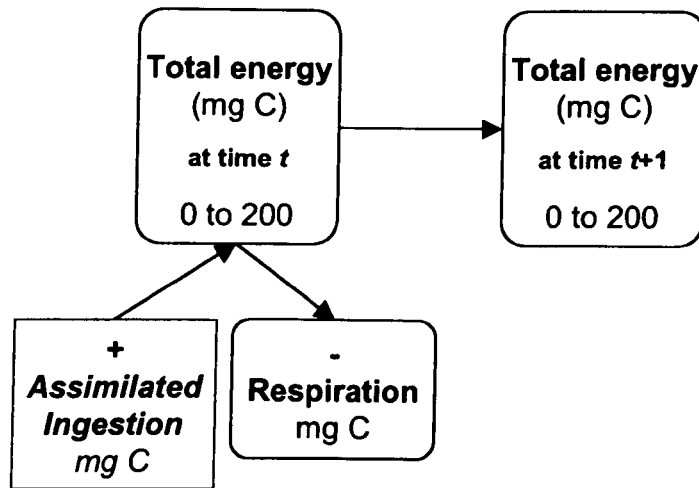


Figure 3.8. Flow chart showing how krill energy changes each time step. Total energy increases from ingestion of phytoplankton, multiplied by assimilation of 0.8, and decreases with respiration. Total energy reserve does not fall below 0 or go above the maximum of 200mg C.

Forward iteration

The model was then run forward for $n = 10\,000$ krill separately. At the start of the time period, each krill was randomly seeded onto the landscape, such that there was an equal concentration of krill in each of the zones. Each krill was also randomly assigned a size m that did not change over the period of the model run. The model ran for $T = 1500$ hours. At each time step krill had an opportunity to eat and respire, with some probability of death. Krill choose the optimum depth, density and swimming behaviour at each time step; maximising fitness depending on the state of the krill in terms of energy level, size and zone, determined by the backward iteration. Following these activities, there was some probability that krill would move to another zone, which depended on depth and swimming decision. A random number was generated, and referenced to the range of probabilities for changing from the current zone z to the new zone y . If the krill moved out of bounds of the defined model area then this was recorded, and the krill was not considered further in the results. If within the bounds of the model, the new position, energy state, depth, swimming decision and swarm density

of the krill were recorded at each time step, and the entire process repeated until the final time T .

Model runs

The model was run firstly with the best estimate parameters, those described in the previous section (Table 3.1). Secondly, each of the main parameters of the model, mortality, advection and swimming decision, were excluded in turn from the model, taking results with and without these parameters. Thirdly, the model was run with best estimate values but different functions for the terminal reward. Finally, a sensitivity analysis was performed to test the robustness of the model. Five parameters were tested in the sensitivity analysis over a range of values, and were chosen either because of their likely influence on model predictions or because a lack of data made a parameter particularly hard to define.

Testing the terminal reward

The first terminal reward tested was that already described in the previous section, where krill must accumulate a threshold amount of energy, based on observed growth rates at South Georgia, in order to obtain a fitness reward at the final time (Equation 3-4 and Equation 3-5). Below this threshold, fitness was zero. The second type of terminal reward tested, terminal reward 2, was where fitness at the final time was equal to zero for all values of accumulated energy e . Instead, each time step fitness accrued by the quantity of food ingested, by adding X_i to the fitness function (Equation 3-19). There are many examples where fitness accrues during each period, such as the oviposition behaviour of insects encountering and laying eggs in hosts in each period (Mangel and Clark, 1988). The resulting terminal reward was therefore

Equation 3-18 $F(T) = 0$

with fitness each time step modified from the previous (Equation 3-16), such that

Equation 3-19
$$F(e, m, z, t) = \max_i \sum_{y=1}^3 Pzone(d'_i, a'_i, z, y) \cdot (1 - \beta_i) \cdot [F(e'_i, m, y, t + 1) + X_i]$$

where X_i was the assimilated ingested food (Equation 3-8). For all other parameterisations of the fitness function, X_i was equal to zero and therefore not considered in the fitness equation.

The third terminal fitness reward tested, terminal reward 3, described a situation where fitness had a simple linear relationship to accumulated energy. This type of terminal reward describes a situation where krill simply maximise energy intake while minimising predation, where there is no threshold energy balance in order to obtain a fitness reward. In this example, there is an expected benefit to fitness with increasing levels of energy, which may result in higher numbers of offspring or higher chance of survival for parents or offspring, or both (Mangel and Clark, 1988).

Equation 3-20 $F(T) = e$

Fitness per time step for terminal reward 3 was calculated as in the best estimate parameterisation (Equation 3-16).

The sensitivity analysis

Some parameters in the model have been more studied than other. Sensitivity analyses were therefore carried out to consider how much the predictions of the model depend on values that are less certain behaviour of the lack of available data. (i) Mortality relating to swarm density was tested in the sensitivity analysis because there is no available quantitative data on how mortality is reduced from being in a swarm. (ii) There are similar uncertainties relating to mortality between zones, for although there are some estimates of predator densities changing with distance from island around South Georgia, many of these are extrapolated from satellite tracking data or ship survey estimates. In addition predator densities can change year to year so it is interesting to see how much of an effect this has on krill behaviour. (iii) The energetic saving from being in a swarm has been widely hypothesised but direct evidence for Antarctic krill is presently weak. (iv) The respiration conversion was tested because there are alternative values for this parameter present in the literature (Hofmann and Lascara, 2000; Ritz, 2000; Ritz et al., 2001; Swadling et al., 2005). The other value tested in the sensitivity analysis was 0.4217, based on a conversion of 46 Joules per mg organic C (Salonen et al., 1976), and 19.4 Joules per ml O₂ respired (Elliot and Davidson, 1975). (v) Finally, phytoplankton availability was varied in the model because phytoplankton is patchy in space and time, and krill have evolved to deal with different scenarios of food availability. It is important to look at the response of krill to these changing conditions in terms of behaviour and the relative importance of phytoplankton availability to small-scale krill decisions.

Table 3.18. Parameters tested in the sensitivity analysis of the model, with values tested.

Symbol	Parameter	Values tested	Units
10^y	(i) Mortality: swarm density (log odds factor see Table 3.15)	(0,0,0) (-0.3,0,0.3) (-0.5,0,0.5) where values (a,b,c) inside brackets represent 10^a , 10^b , 10^c for swarm densities low, medium and high respectively	-
10^y	(ii) Mortality: zone (log odds factor see Table 3.15)	(-0.3,0,0.3) (-0.5,0,0.5) (-1,0,1) where values (a,b,c) inside brackets represent 10^a , 10^b , 10^c for swarm densities low, medium and high respectively	-
Rdensity(s)	(iii) Energetic saving: swarm	(0,0.9,0.8) (0,0.8,0.6) (0,0.7,0.4) where values (a,b,c) represent the reduction in respiration for low, medium and high swarm densities (see Equation 3-9)	-
Rc	(iv) Respiration conversion	0.5357 and 0.4217 (see Equation 3-9)	-
Phyt(d,z)	(v) Phytoplankton availability	see (Figure 3.5) and (Table 3.12)	mg C m ⁻³

RESULTS

Best estimate model

The following section contains results from model simulations of both high and low phytoplankton availabilities, with all other parameters set at their best estimation. In general, results are divided into size and zone, to see if krill of a different size or in a different area exhibit contrasting behaviours. Although the model was run for a total of 1500 hours, 2 months, only the middle month is represented here (see Methods).

Predicted behaviour

The behaviour of small and large krill was predicted by the model in terms of depth, density, swim speed and turn rate in each of the zones. As krill are known to adopt some diel behaviours, many of the results were divided into day and night.

When the model was run with a high availability of phytoplankton, the depth and density of small and large krill on-shelf followed a similar trend, with the model predicting deep high density swarms for all krill during the day and most krill during the night (Figure 3.9). With a low phytoplankton availability, the behaviour of small krill was again similar to large krill, but this time the model predicted a classic DVM on-shelf with mostly deep high density swarms during the day, and shallow low density swarms at night (Figure 3.9). At the shelf-break zone in the simulation with high food availability, the model predicted a DVM where small and large krill were in low-density swarms both day and night (Figure 3.9). DVM at the shelf-break was also predicted with a low availability of phytoplankton, but with high density deep swarms during the day (Figure 3.9). Off-shelf, the trend was different between sizes, but similar over differing food levels (Figure 3.9). Small krill in the model exhibited a pattern of DVM, deep high density during the day and shallow low density during the night for both high and low food simulations (Figure 3.9). Large krill could be found in deep high density swarms during the day, with one third to half of the large krill also in deep high density swarms during the night, the rest in shallow low density swarms (Figure 3.9).

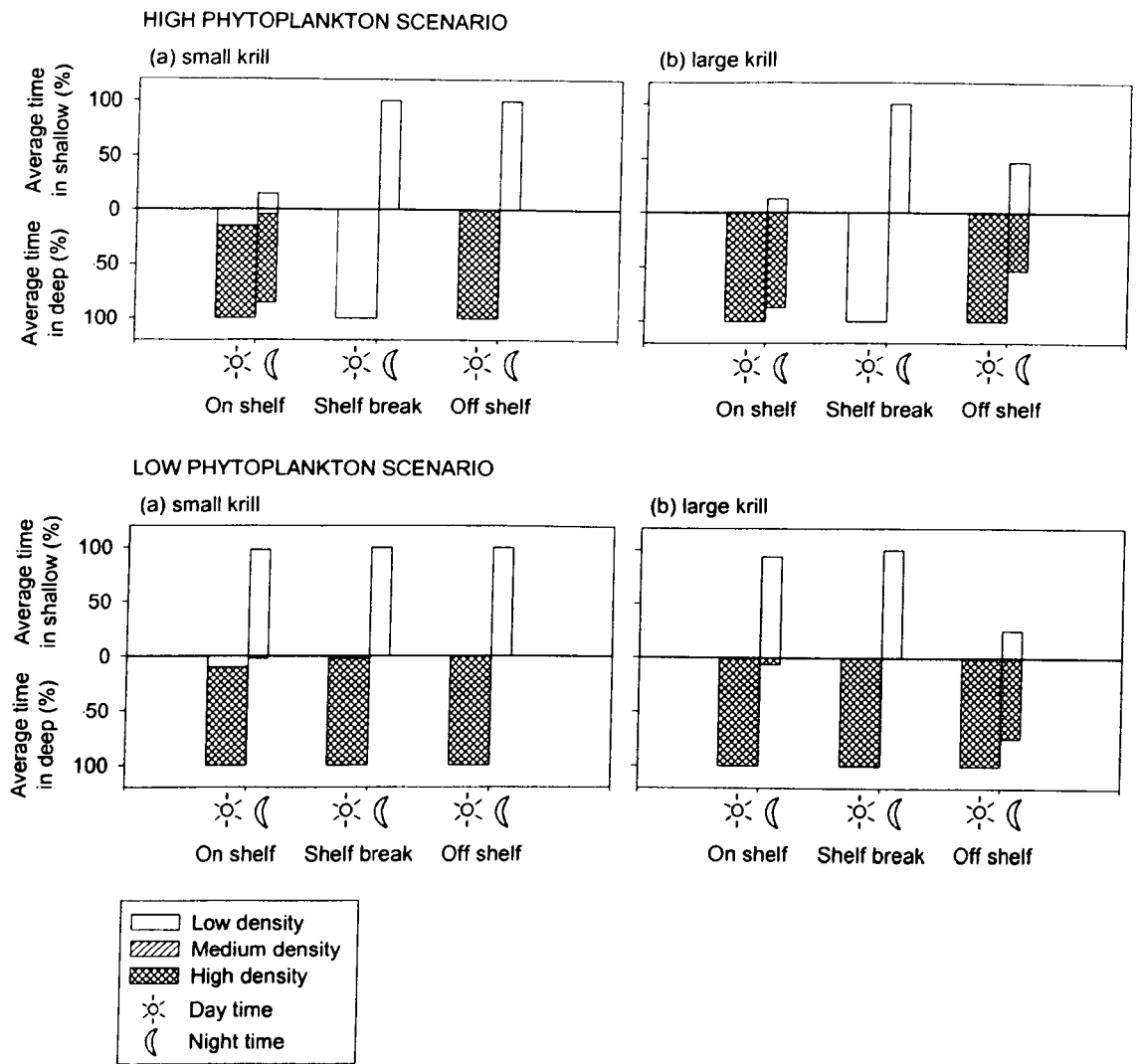


Figure 3.9. The predicted average depth and density of small and large krill, for day and night in each of the zones, and for simulations of both high and low phytoplankton availability.

The model also predicted the behaviour of krill in terms of swimming speed and turn rate, affecting the likelihood of krill dispersing from- or retaining themselves within an area. This swimming behaviour was divided into three types, classed as swimming randomly (random speed and turn rate), swimming to stay in an area (low speed, high turn rate) and swimming to disperse from an area (high speed, low turn rate), described in the model as random, stay or disperse, respectively.

With high phytoplankton availability, both small and large krill adopted a swimming behaviour that increased the probability of dispersing away from the on-shelf and off-shelf zones, but maximised the probability of retention in the shelf-break zone (Figure 3.10). With low food availability, the predicted krill behaviour at the shelf-break and off-shelf was the same as with high food availability. However, the behaviour differed on-shelf, with most small krill (around 80%) and all large krill adopting a swimming behaviour that would increase the probability of staying in the zone as opposed to a dispersal behaviour observed when food availability was high. The model predicted that no krill in the best estimate parameterisation chose to swim with a random speed and turn rate, for either high or low phytoplankton availability.

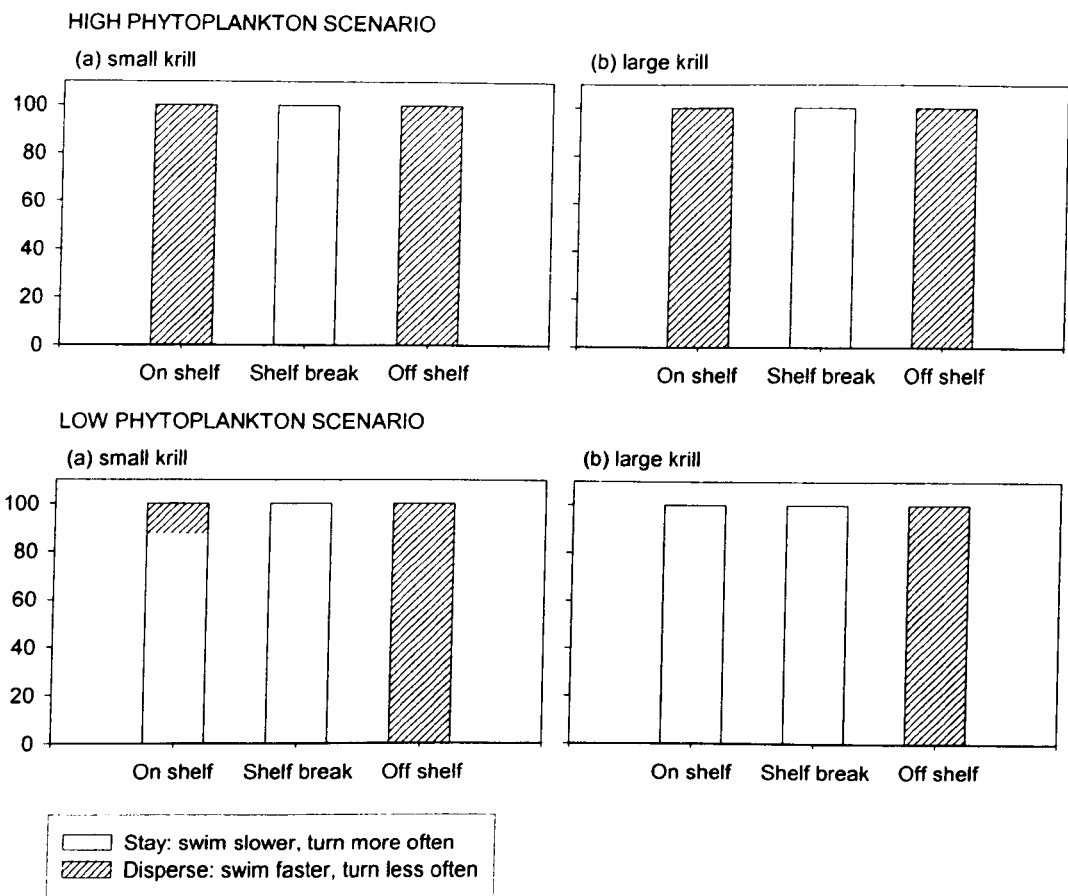


Figure 3.10. Krill swimming behaviour in terms of swimming speed and turn rate, according to rules for random swimming, swimming to stay in zone, and swimming to disperse from zone. Results were averaged from simulations with high and low phytoplankton concentration

Predicted energy levels

Results show the average accumulated level of energy assimilated each day for 10000 krill, increasing with intake of phytoplankton and decreasing with respiration. The results were divided into krill of different zones and sizes, and for model simulations of high and low phytoplankton levels.

Krill accumulated energy linearly over time when there was a high availability of phytoplankton in the model, except on-shelf where the average increase in energy was more sporadic due to there being very few krill remaining in this zone (Figure 3.11).

Both small and large krill accumulated the greatest amount of energy in the shelf-break zone, and the least amount of energy on-shelf. In all zones, krill were able to reach their target growth rate by the final time. Small krill reached an energy level approximately equal to that of large krill in all model regions except the shelf-break, where large krill accumulated almost twice the energy of small krill.

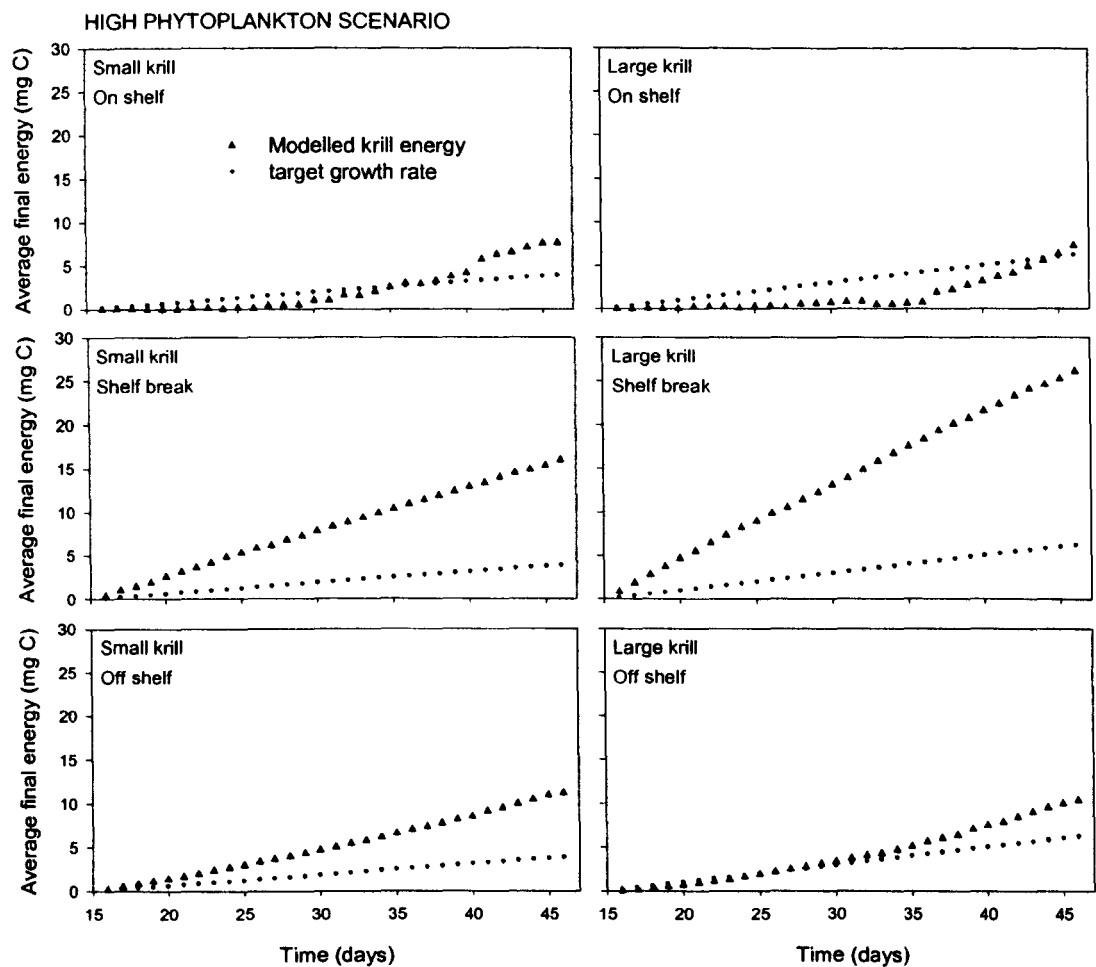


Figure 3.11. Average energy levels of krill, from day 16 to 46, divided into size class and regional zone, with high phytoplankton levels. The target growth rate was based on net samples in the South Georgia area (Atkinson *et al.* in press).

With low phytoplankton availability, krill accumulated less energy overall (Figure 3.12) compared to the high phytoplankton scenario. With less food, only small krill were able to reach their target growth rates, and only on-shelf and at the shelf-break. Large krill

came closest to their target growth rates on-shelf, doing least well off-shelf. All krill accumulated the most energy on-shelf and the least energy off-shelf. Even though the energy accumulation over time was very slow in some zones, it was always positive.

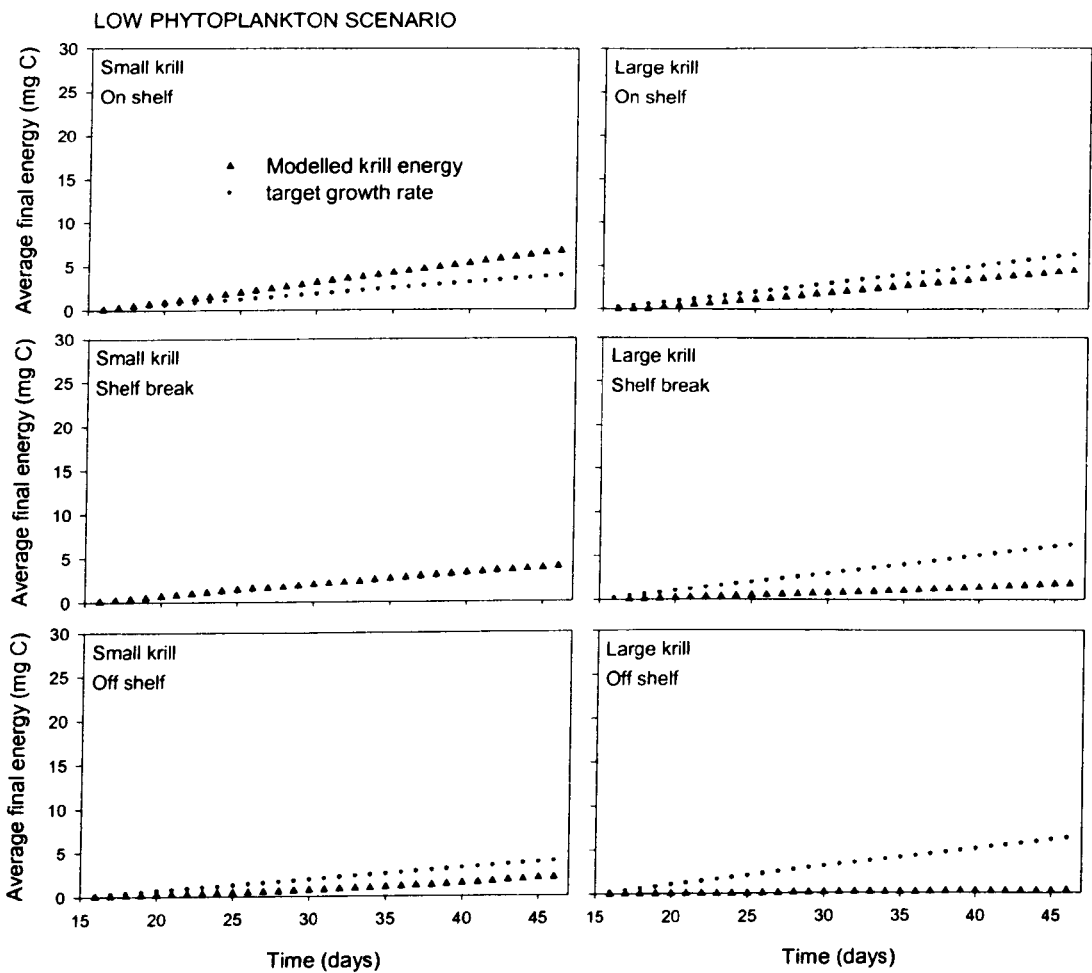


Figure 3.12. Average energy level of krill at the end of each day, from day 16 to 46, divided into size class and zone, with low phytoplankton levels. The target growth rate was based on net samples in the South Georgia area (Atkinson *et al.* in press).

Compared to a low phytoplankton year, the final energy level of krill in a high phytoplankton year was more than twice the change in concentration of phytoplankton. In some zones, krill were able to increase their energy levels up to nine fold with only twice as much phytoplankton available (Figure 3.11). This is because by changing their

behaviour to low density swarms day and night, krill were able to take advantage of the higher food levels (Figure 3.9).

Predicted distribution of krill

The krill distribution results are presented in terms of krill concentration, calculated by dividing the total number of krill in a region by the total area (m^2) of the region, to give giving krill m^{-2} . It was necessary to compare the concentration of krill because the area covered by each of the three regions was considerably different. However, this represents a nominal scale to be treated in a relative fashion and is not a prediction of the real concentrations expected in those zones.

The number of krill in all regions declined over time (Figure 3.13). This is because the krill were diffusing out of the model area, from which point they could not re-enter the simulation. This effect commenced on model day 1, which explains why concentrations on day 15 are already unequal. What is also clear is that this effect is not as strong at the shelf-break as in the other 2 regions such that, by the end of the simulation, concentrations at the shelf-break are comparatively high. The concentration of krill was similar for large and small krill in all regions for the model.

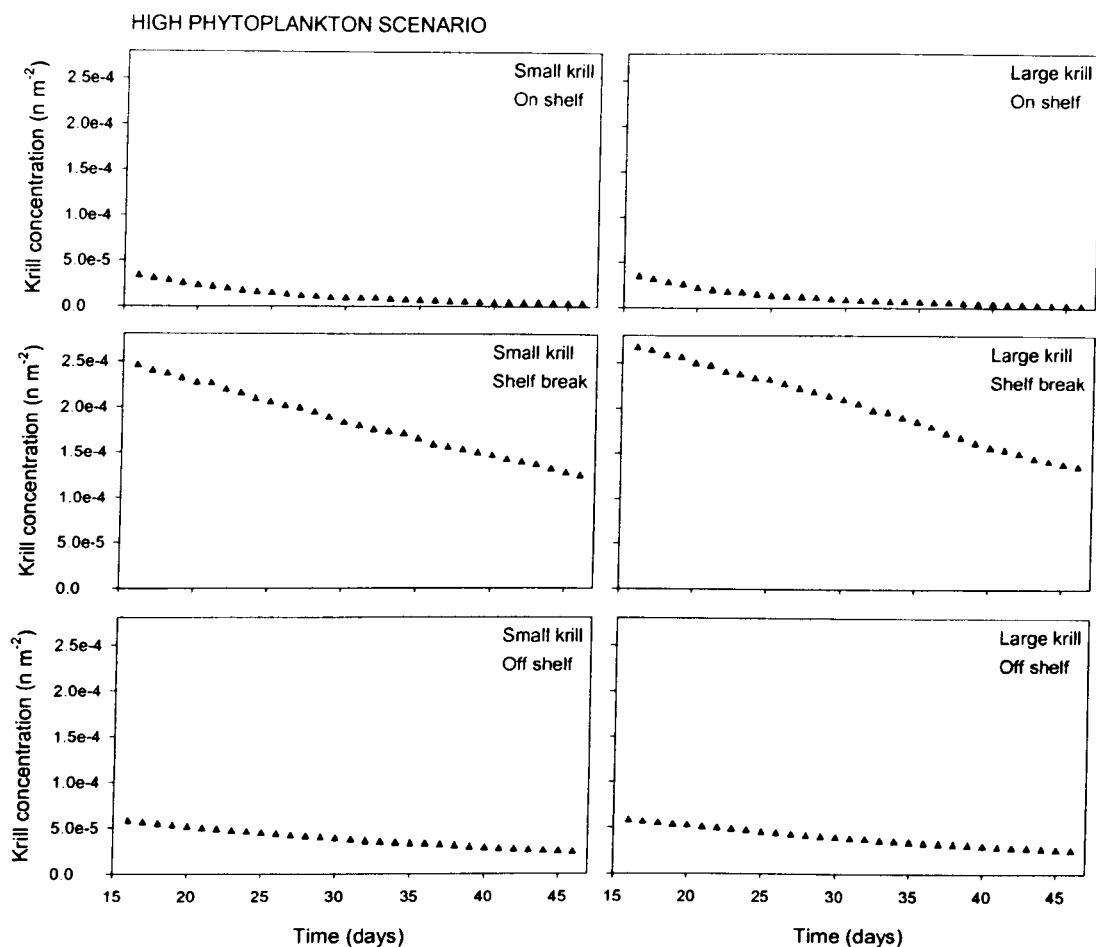


Figure 3.13. Krill concentration over time, in krill m⁻², for a simulation with high phytoplankton. The target growth rate was based on net samples in the South Georgia area (Atkinson *et al.* in press).

The pattern in krill concentration was similar for the simulation with low phytoplankton availability, differing only in the concentration of large krill on-shelf (Figure 3.14). Here, the concentration of large krill started at a level around three times higher than with that high food availability, and although declining gradually over time, stayed at a relatively high concentration. In addition, small krill on-shelf, although at a low concentration throughout the model period of interest, stayed relatively constant over time. Off-shelf, the concentration of both large and small krill was low and decreased steadily over time, similar to the simulation with high phytoplankton availability.

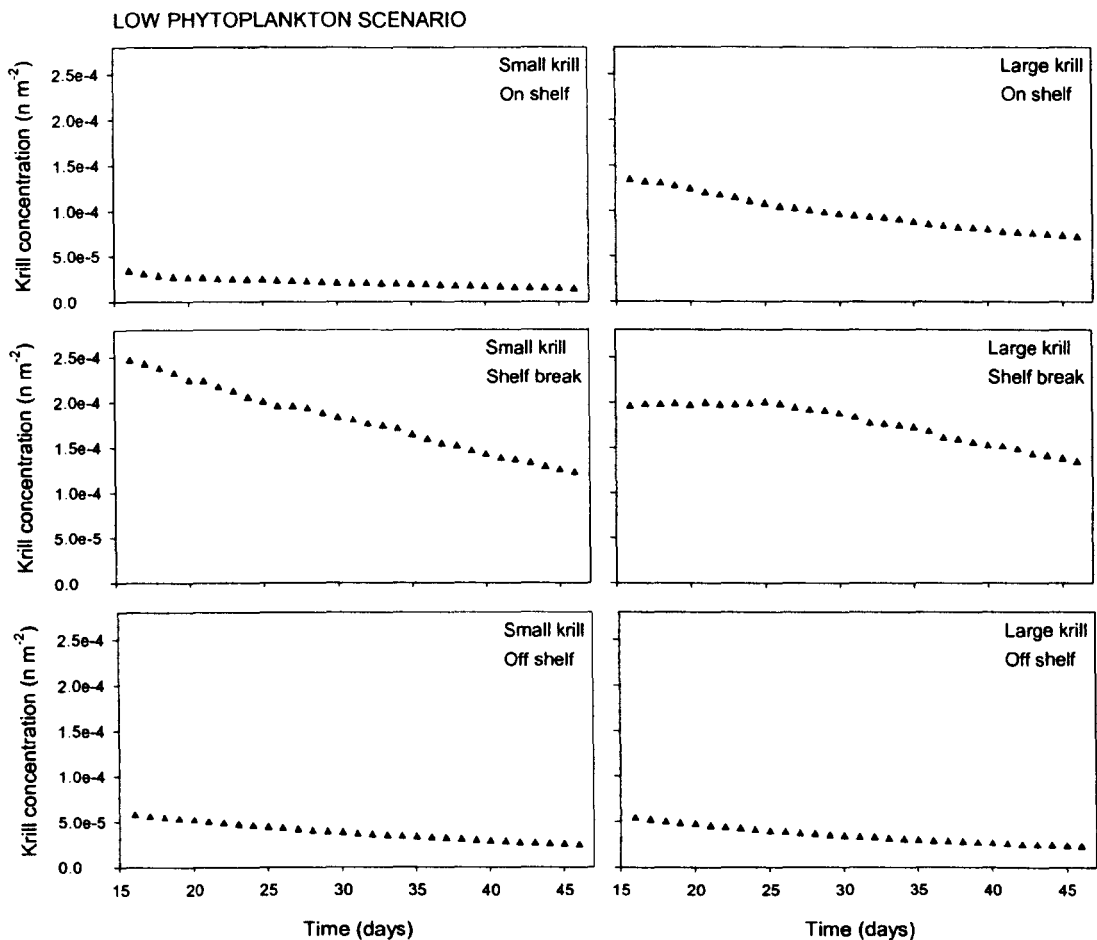


Figure 3.14. Krill concentration over time in simulation with low phytoplankton availability.

Examining the final concentrations of krill at day 46, krill concentration was clearly the highest in the shelf-break region for all simulations, consistently at least four times greater than off-shelf (Figure 3.15). On-shelf, there were differences between size and year, with both small and large krill almost absent with high food availability. With low food availability, the concentration of small krill on-shelf was around half that off-shelf, and the concentration of large krill was close to three times greater on-shelf than off-shelf.

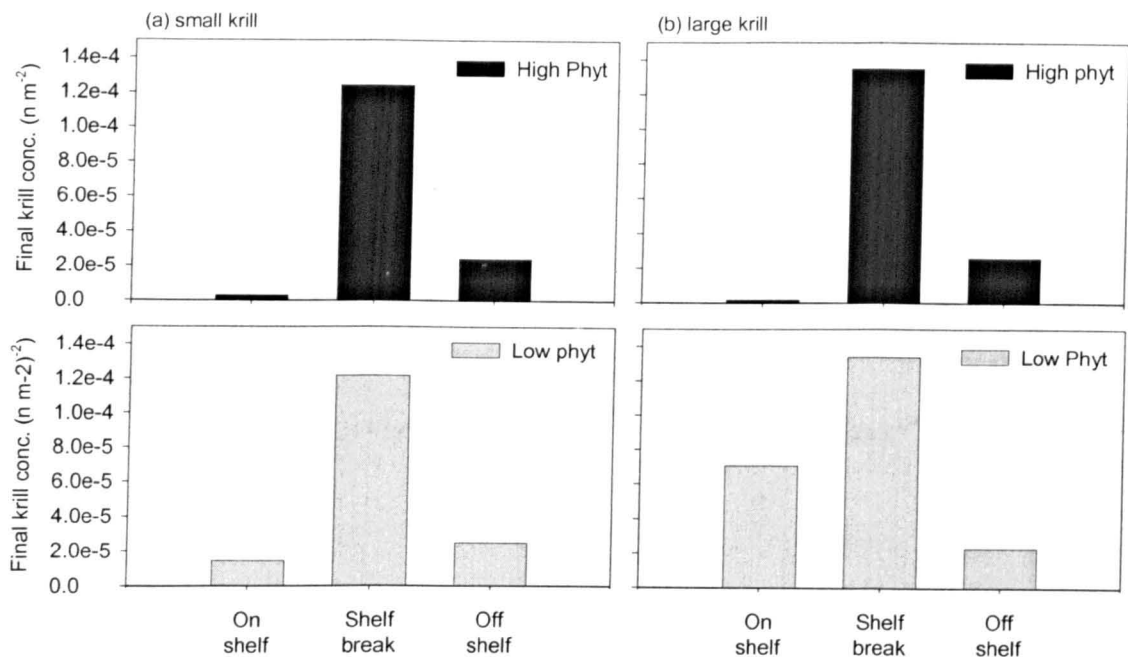


Figure 3.15. Final krill concentration in each of the zones for small and large krill, and simulations with low and high food concentrations.

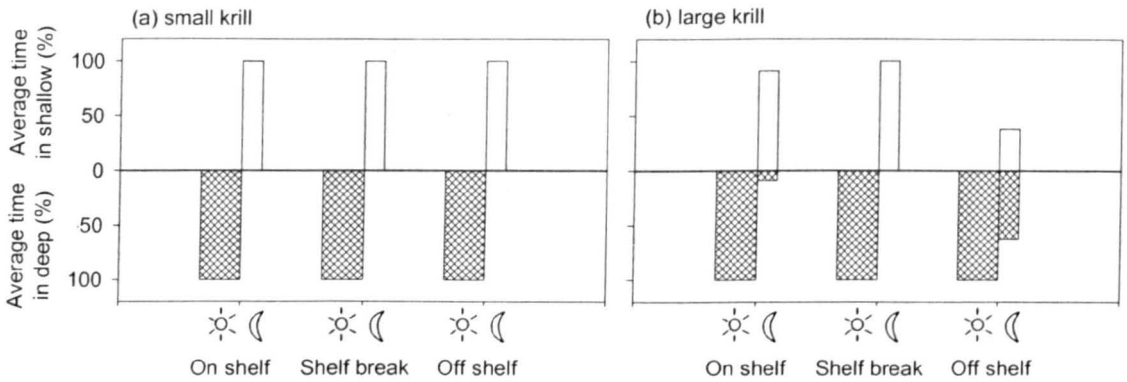
Changing the terminal reward

This section deals with changes to the terminal reward function and how these changes affect the behaviour of krill with any resulting changes to krill distribution and energetic intake. Results (Figure 3.16 to Figure 3.19) show the effect of changes in the terminal reward for high and low phytoplankton availability, and for small and large krill. There is a set of results for each of the simulations with a differing fitness function, with all other parameters at their best estimate values. Terminal reward 1 is that used in the previous section for best estimate results, where there is a target amount of energy, above which there is a fitness reward and below which there is no reward. Terminal reward 2 is where fitness at the final time step is zero, but fitness is accrued each time step when krill eats. The final terminal reward tested, terminal reward 3, is where krill simply try to maximise the amount of food intake.

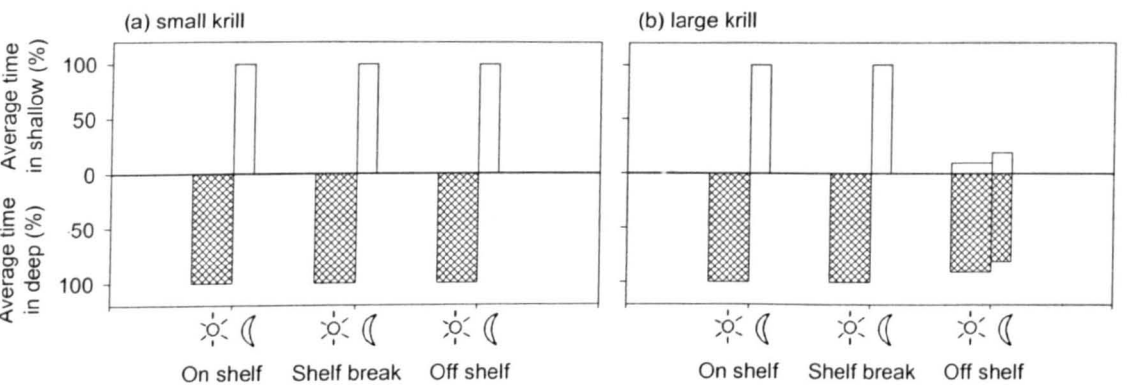
Predicted krill behaviour, in terms of depth and density, is presented for low and high phytoplankton scenarios. With low phytoplankton availability, a model with terminal reward 3 resulted in krill behaviour that differed most to the other two scenarios tested, particularly on-shelf (Figure 3.16). In this instance, a much greater proportion of krill were deeper in the water column at night than in the other two scenarios, representing a less risky behaviour choice. This also occurred off-shelf, although the proportion was smaller. The behaviour of krill at the shelf-break did not change with parameterisation of the terminal reward except for large krill in the model terminal reward 3, again adopting a less risky behaviour at night.

LOW PHYTOPLANKTON SCENARIO

TERMINAL REWARD 1



TERMINAL REWARD 2



TERMINAL REWARD 3

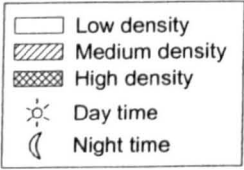
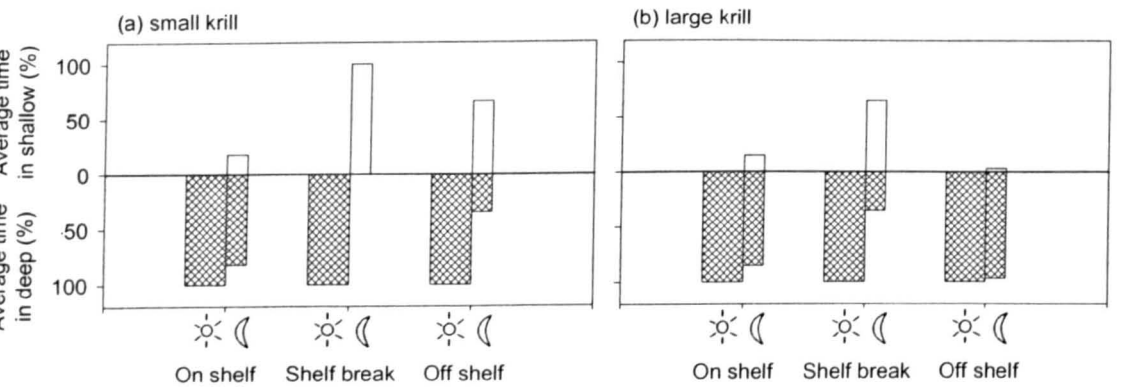
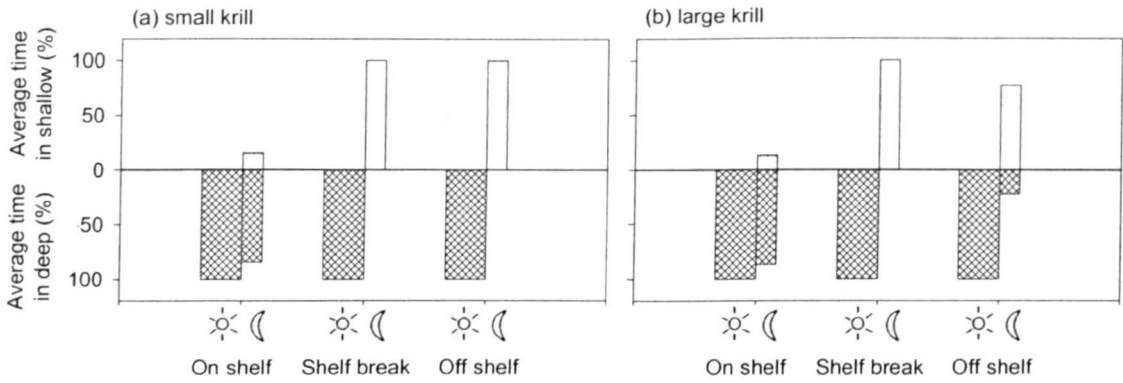


Figure 3.16. The sensitivity of predicted krill behaviour in the model to three different terminal reward functions. Plots show depths (shown by vertical bars) and densities (shown by hatching on bars) adopted in different regions (on-shelf, shelf-break and off-shelf) by small and large krill. Results are for a model with low availability of food.

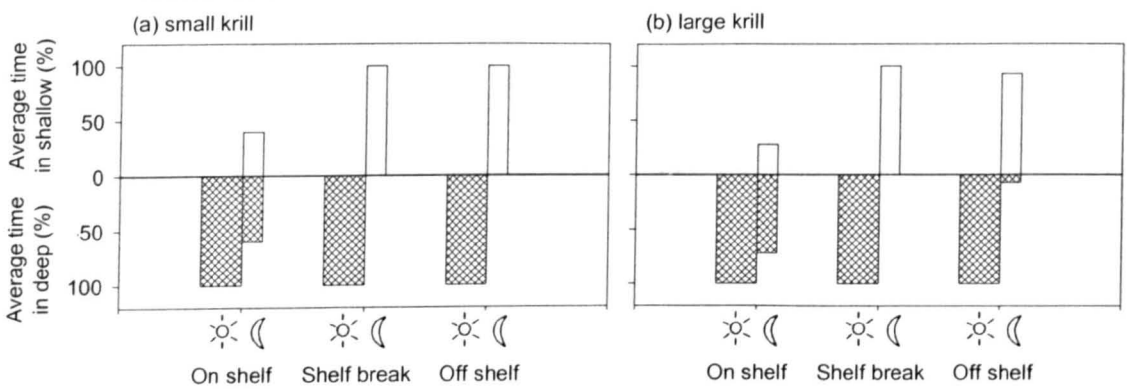
With high phytoplankton availability, the difference between the three models was less noticeable (Figure 3.17). In general, the model predicted a less risky behaviour (reduced exposure to predation risk) for krill with terminal reward 3, with krill deeper and denser. This contrasted to a prediction of more risky behaviour for krill with terminal reward 2, with a higher proportion of krill in shallow low-density swarms. The predicted behaviour at the shelf-break did not change with different parameterisations of the terminal reward.

HIGH PHYTOPLANKTON SCENARIO

TERMINAL REWARD 1



TERMINAL REWARD 2



TERMINAL REWARD 3

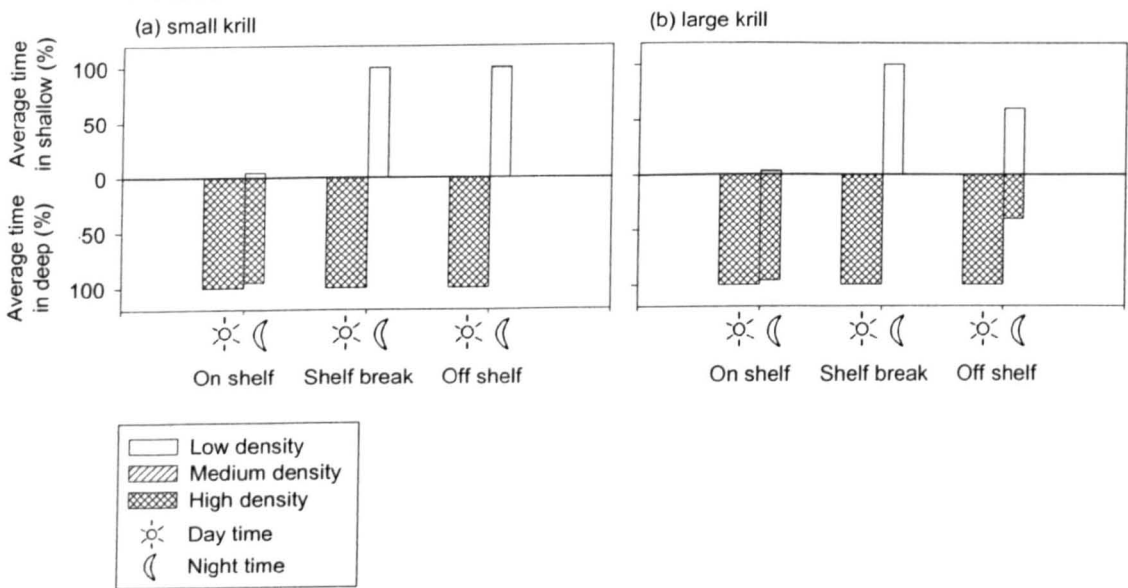


Figure 3.17. The sensitivity of predicted krill behaviour in the model to three different terminal reward functions. Plots show depths (shown by vertical bars) and densities (shown by hatching on bars) adopted in different regions (on-shelf, shelf-break and off-shelf) by small and large krill. Results are for a model with high availability of food.

The average final energy level for krill after 46 days of simulated behaviour allows a comparison of scenarios for both high and low phytoplankton availability and for each of the parameterisations of terminal reward (Figure 3.18). The difference between the final energy level of the three terminal rewards was more pronounced for low phytoplankton availability than high. Krill gained the highest average energy with terminal reward 2, where fitness accrued with ingestion, and the lowest average energy with terminal reward 3, where there was no target growth rate but a linear terminal fitness reward.

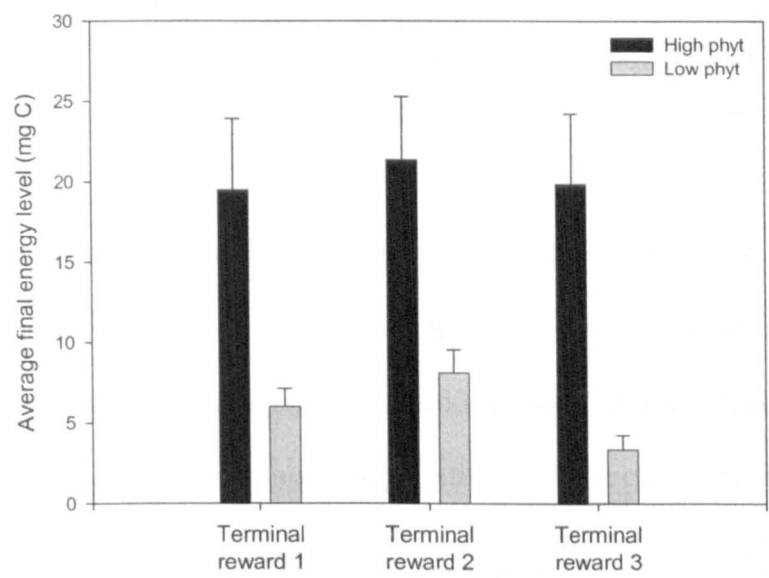


Figure 3.18. Average final energy level (\pm S.E.) for 3 models with different terminals rewards, and for low and high availability of phytoplankton.

The effect of changing the terminal reward on krill concentration in each of the zones was most noticeable on-shelf when phytoplankton availability was low, with more krill remaining in this high mortality, high food zone for terminal reward 2 compared to 1 and 3 (Figure 3.19). At the shelf-break and off-shelf the effects were less noticeable.

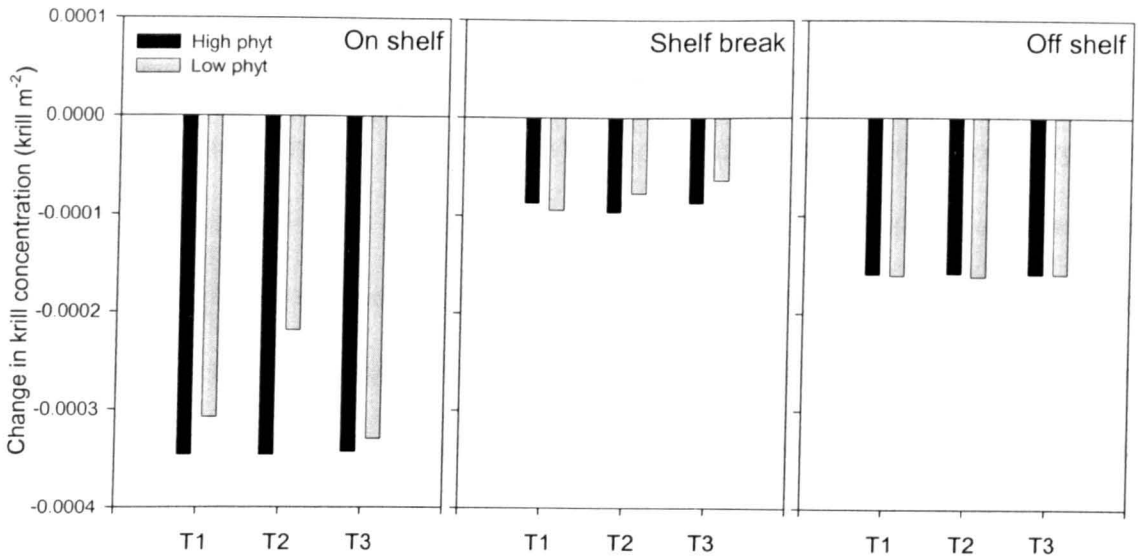


Figure 3.19. Changes in krill concentration in each of the zones of the model, for a model with terminal reward 1, terminal reward 2 and terminal reward 3 (T1, T2 and T3 respectively). The result for high and low availability of phytoplankton is also shown.

The results from this section indicate that differences in results between models with differing terminal rewards were not great, but there were some general patterns. A model with terminal reward 2, where fitness accrued with ingestion, led to the most risky behaviour both in terms of a greater proportion of shallow low-density swarms and more krill adopting a swimming behaviour that led to accumulation on-shelf, the region with highest food and predation risk. This logically led to a higher accumulation of energy. In contrast, behaviour for a model with terminal reward 3, with a simple linear fitness function, was the least risky predicted, with a greater proportion of deep high-density swarms leading to a lower final energy state. The difference between the terminal reward predictions was most noticeable when phytoplankton availability was low, probably because krill were under more pressure to reach their terminal rewards.

Workings of the model

This section deals with a means of testing the working of the model, in which some parameters were completely removed then re-added to the model to determine their effects on the results. All other parameters, other than those removed or added, were set to best estimate values for each of the simulations. By examining the structure of the model in this way, it was possible to determine which parameters were important in the model, and how they affected krill behaviour. Mortality risk, advection and a choice of swimming speed and turn rate were completely removed then returned to the model, while food concentration was varied as in the previous section. The effects on the model were examined in terms of krill energy levels, relative krill concentration in each region, and krill behaviour in terms of diel depth.

Effects of food concentration, mortality risk, behaviour choice and advection on energy intake

The results presented in the following figure show the average final energy level for krill at day 46, the end of the model period of interest (Figure 3.20). The energy levels of krill transported out of bounds before the final time were not included in the average. The overall energy acquired by krill in simulations excluding mortality was four or more times greater than when mortality was included. In addition, the average final energy level with high food availability was mostly around twice that with low food availability. The choice of swimming speed and direction (choice/no choice) had a smaller impact on final energy levels, with a noticeable effect only when advection was included in the model (C2). With advection (C2) and without mortality, krill with a choice of swimming speed and direction were able to influence their position, resulting in around a 25% increase in energy compared to krill that could not influence their

position in this way. With mortality and advection (C2), the increase in average krill energy from having a choice of swimming speed and direction was similarly around 25% for high food simulations, but no difference for low food simulations.

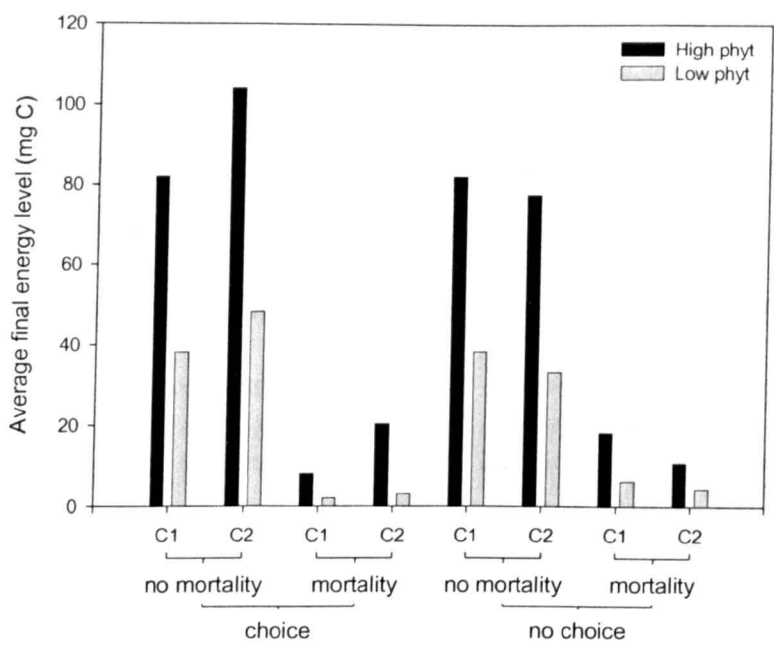


Figure 3.20. Comparing average final energy for 10000 krill, over high and low food levels, with differing model structure. ‘Choice’ indicates whether krill could alter swimming behaviour to influence advection. ‘Mortality’ indicates whether the model included a risk of mortality. ‘C1’ represents model runs without advection, where krill could not change zones. ‘C2’ simulations that included advection; current speeds were included and krill had some probability of changing zones each time step.

Effects of food concentration, mortality risk, behaviour choice and advection on krill distribution

The following figures examine the effect of changing model structure on krill distribution in each of the zones, indicating the difference between the initial and final number of krill. The results represent an average for both small and large krill. In addition, there are no results here for model simulations without advection (C1) since this model is only concerned with scenarios where distributions change over time.

Including or excluding a choice of swimming behaviour in the model ('choice'/'no choice') had a different effect on the relative change in krill concentration in each of the zones (Figure 3.21). A greater concentration of krill was transported out of the off-shelf region when krill were able to influence their position ('choice'), compared to simulations where they had no choice. In contrast, more krill were retained at the shelf-break region when krill had a choice of swimming speed and turn rate, especially when mortality was also included in the model (Figure 3.21). Including mortality had a less noticeable effect on krill distribution than final energy level, although the inclusion of mortality did result in a lower concentration of krill on-shelf and a higher concentration at the shelf-break. The distribution of krill in all zones was similar for simulations of high and low phytoplankton availability.

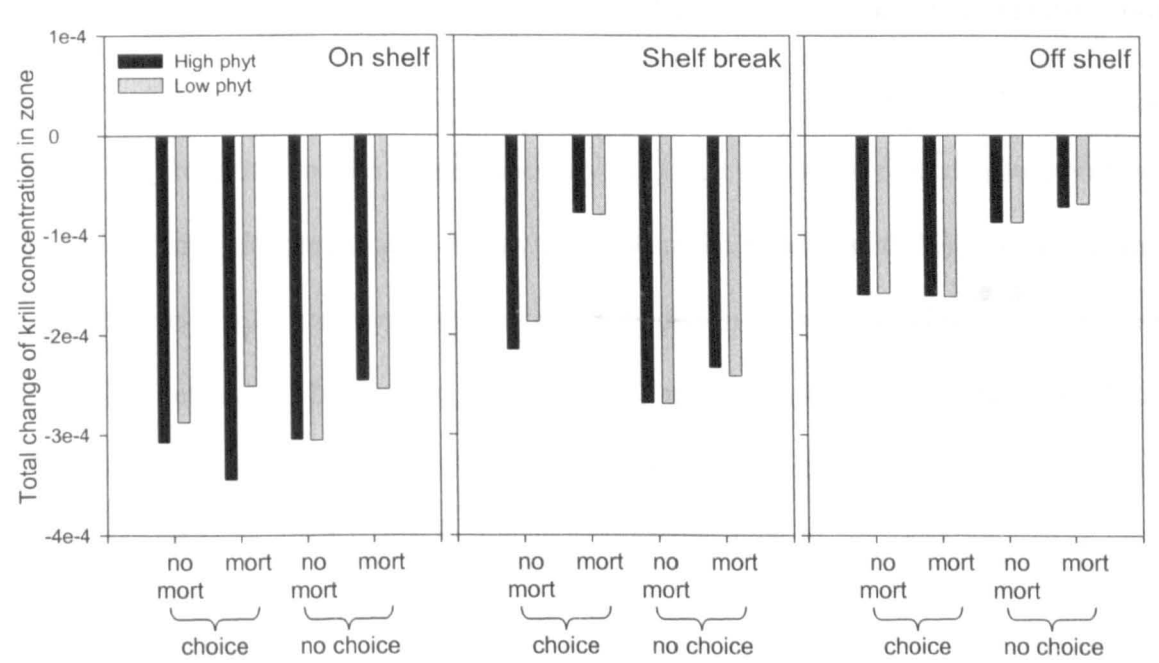


Figure 3.21. Average change in the concentration of krill in each zone.

*Effects of food concentration, mortality risk, behaviour choice and advection on krill
depth*

The following figures show krill behaviour in terms of average depth for the entire month, divided into day and night.

Krill spent all their time in the shallow water, both day and night, when mortality was not included in the model (Figure 3.22). With mortality in the model, most individuals spent daytime at depth irrespective of food availability and advection. In model simulations where krill had an opportunity to influence their advection ('choice'), krill depth at night was deeper than in simulations without a choice of swimming behaviour, especially with high food availability. Similarly, krill depth during the day was shallower when krill had an opportunity to influence their position, particularly when food concentration was low (Figure 3.22).

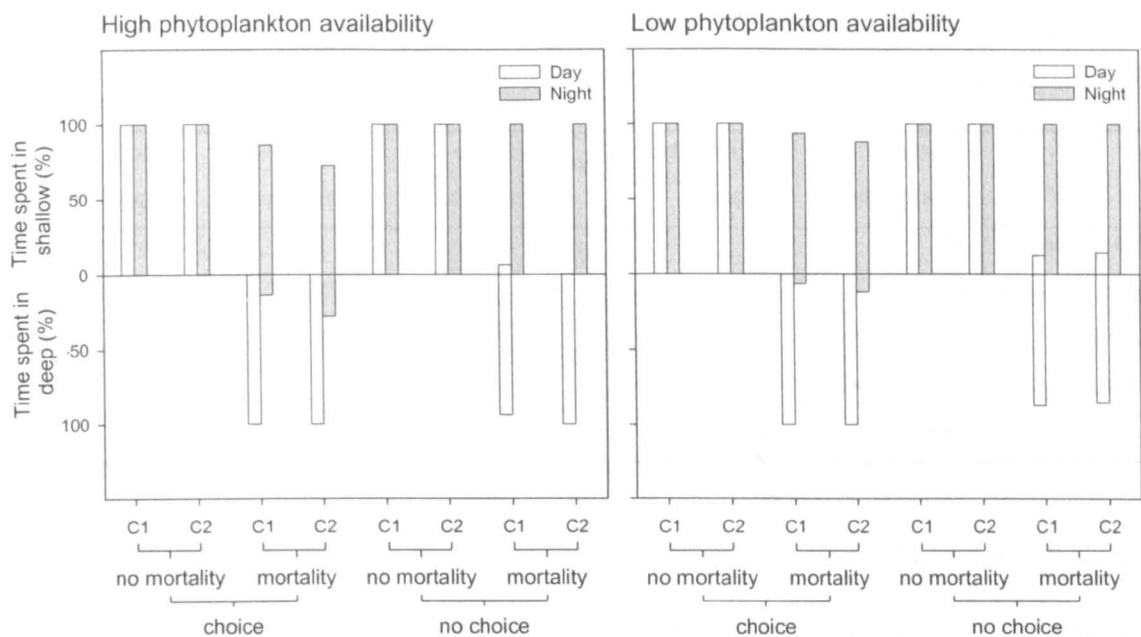


Figure 3.22. Overall proportion of time spent in shallow water over the model month, divided into day and night for simulations of both high and low levels of phytoplankton. ‘C1’ and ‘C2’ are model simulations without and with advection respectively. ‘Choice’ specifies whether krill in the model had a choice of swimming speed and turn rate. ‘Mortality’; whether a risk of mortality was included in the model.

The results from this section reveal primarily the large effect that mortality had on both the behaviour and accumulated energy of krill in the model, with krill accumulating much more energy when mortality was not included in the model. Having a choice of swimming behaviour also influenced the results, but to a lesser extent, with krill able to accumulate more energy when they could influence whether or not they moved to or remained within favourable areas.

Sensitivity analysis

There were a number of parameters tested in the sensitivity analysis (Table 3.19) .

Table 3.19. Parameters tested in the sensitivity analysis, with actual values used in each of the different simulations.

	Mortality: Swarm density	Mortality: Zone	Energetic saving: swarm	Respiration conversion	Food availability
No. values	3	3	3	2	2
Values tested	0, 0.3, 1	0.3, 0.5, 1	0, 0.1, 0.2	0.5357, 0.4217	High, low
Values change with	Swarm density, depth, zone, time	Swarm density, depth, zone, time	Swarm density	Krill size	Depth, zone

The total number of simulations run for the sensitivity analysis was 3 x 3 x 3 x 2 x 2 = 108 simulations. To test the sensitivity of each of the parameters, firstly the difference between the result of each simulation and the result of the best estimate simulation was calculated as a percentage of the best estimate result:

Equation 3-21
$$Sensitivity = \frac{(result_{sim} - result_{best})}{result_{best}} \cdot 100$$

Testing was carried out in an hierarchical manner (Figure 3.23) so ensuring all possible combinations of values were considered. Values ranged between their maximum and minimum levels considered in the original parameterisation.

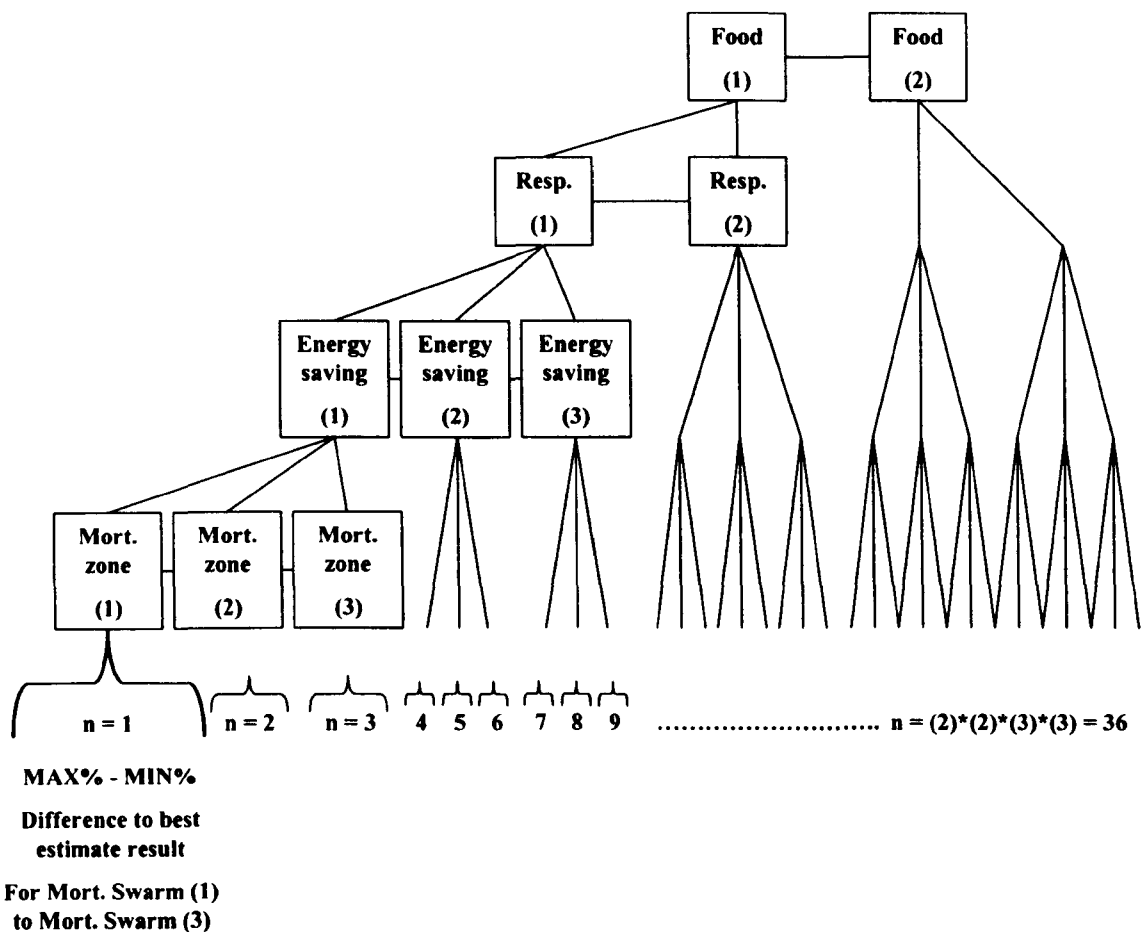


Figure 3.23. Description of the sensitivity analysis, giving the example for testing the sensitivity of mortality relation to swarm density (Mort. Swarm). The value for MAX% - MIN% sensitivity compared to the best estimate was averaged over $n = 54$ simulations for all combinations of the remaining parameters of food, respiration, energy saving and mortality relating to zone (Mort. Zone). The process was repeated for $n = 1$ to 36 for Mort. Zone, $n = 1$ to 36 for Energy Saving, $n = 1$ to 36, Respiration, $n = 1$ to 54, Food/phytoplankton availability, $n = 1$ to 54.

Sensitivity of the final energy level of krill

The following figure shows the sensitivity of the average final energy result. This result was most sensitive to changes in the parameter specifying food availability (45%) and least sensitive to changes in mortality relating to zone and the energetic saving related to swarm density (Figure 3.24). The final energy level was also sensitive to changes in respiration and mortality relating to swarm density (each ~30%) (Figure 3.24).

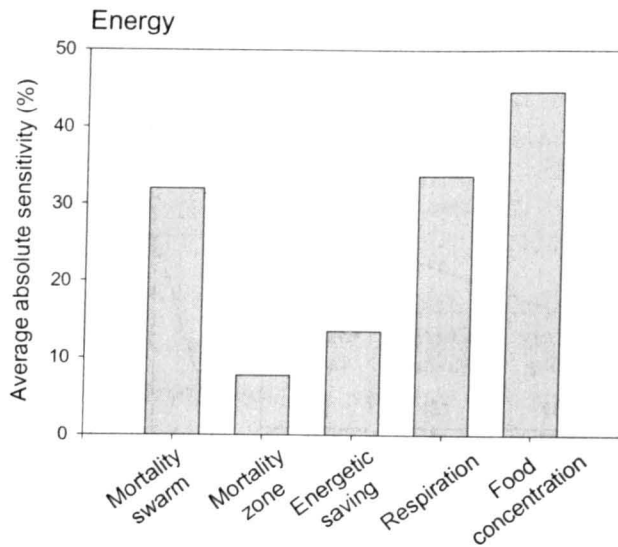


Figure 3.24. Average sensitivity of each of the tested parameters when compared to the best estimate result for the average final energy level for krill.

Sensitivity of the final krill distribution

The sensitivity of the model in terms of the final krill distribution was tested by comparing the final concentration of krill in each of the zones (Figure 3.25). The final concentration of krill, at day 46 in the model, was extremely sensitive on-shelf; an order of magnitude more than any other result tested. In this zone, the final concentration of krill was most sensitive to changes in mortality relating to zone (~600%), and secondly most sensitive to changes in the parameter specifying food availability (~400%). The sensitivity recorded for the on-shelf result was particularly high most likely because the final concentration of krill in this zone was often close to zero, as shown in the best estimate section (Figure 3.13). Comparing, or dividing, a value by a very small value close to zero will result in a much higher estimation of sensitivity. In this case, it is better to compare the relative results for each of the parameters within this zone, and examine the other zones separately.

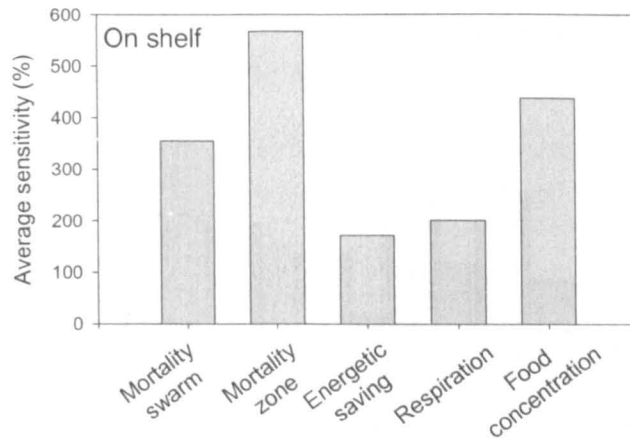


Figure 3.25. Average sensitivity for each of the tested parameters when compared to the best estimate result for final concentration of krill on-shelf.

The final krill concentration result was much less sensitive at the shelf-break and off-shelf compared to on-shelf (max ~15%). At the shelf-break there was a similarly low sensitivity to all parameters tested, ranging from around 5 to 10% (Figure 3.26). Off-shelf, the result was most sensitive to mortality relating to zone (~15%), and secondly to changes in both food availability and mortality relating to swarm density (~10%).

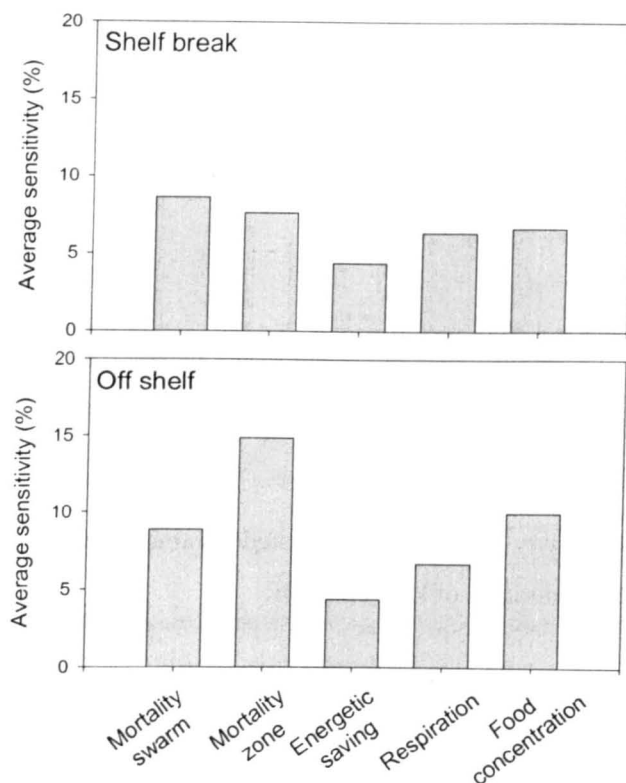


Figure 3.26. Average absolute sensitivity (maximum% – minimum%) for each of the tested parameters when compared to the best estimate result for final concentration of krill on-shelf.

Krill depth result

Both the proportion of krill in the shallow water at night, and the proportion of krill in the deep water during the day were averaged over the month to test the sensitivity of the krill depth result.

The proportion of krill in the shallow water at night was most sensitive to changes in the parameter for mortality relating to swarm density (~12%), which was around twice the sensitivity of the other parameters tested (~4-6%) (Figure 3.27).

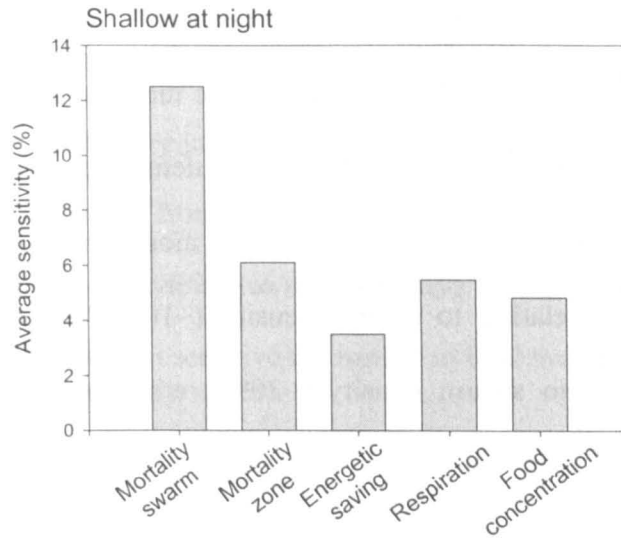


Figure 3.27. Average sensitivity for each of the tested parameters when compared to the best estimate result for proportion of krill in the shallow water at night.

The proportion of krill in the deep water during the day was not sensitive to changes in parameter values, with less than 1% sensitivity for any parameter tested (Figure 3.28).

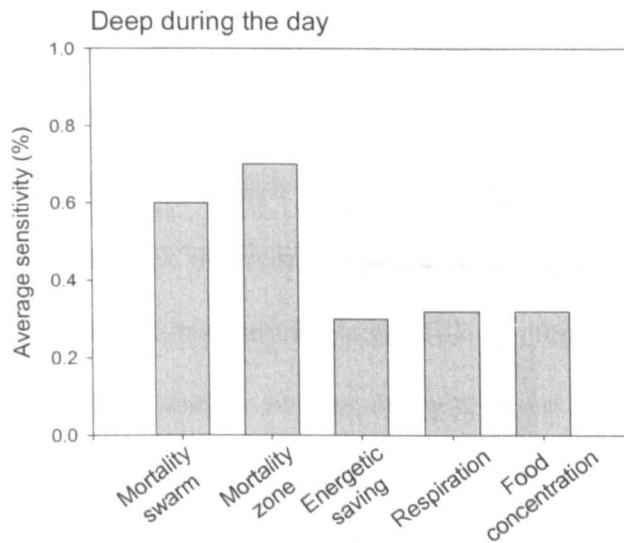


Figure 3.28. Average absolute sensitivity (max – min) for each of the tested parameters when compared to the best estimate result for proportion of krill in the deep water during the day.

Krill swarm density result

The sensitivity of the krill swarm density result in the model was tested by comparing the proportion of individuals in swarms of differing density averaged over the model period. The density of swarm adopted by krill was most sensitive to changes in the parameter for mortality relating to swarm density (~10-30%) and secondly to the energetic saving relating to swarm density (~20%), with the exception of medium density swarms (Figure 3.29).

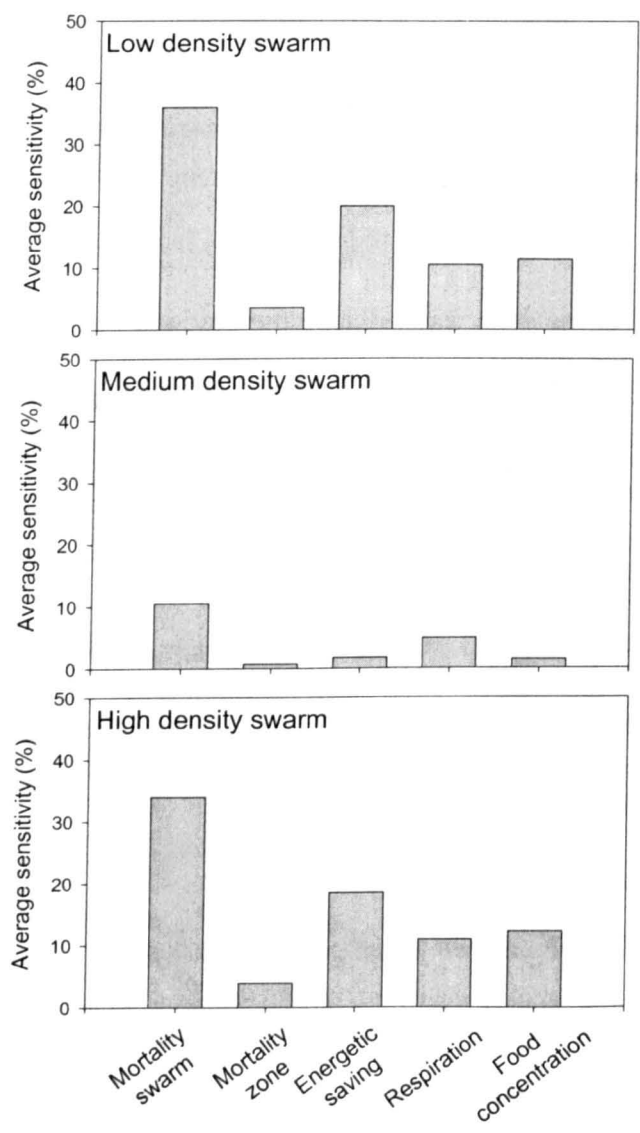


Figure 3.29. Average sensitivity for each of the tested parameters compared to the best estimate result for the average proportion of krill in swarms of low, medium and high.

Generally, results were most sensitive to changes in the parameters defining both mortality and food availability in the model. Results were least sensitive to changes in both the energetic saving from being in a swarm, and the parameterisation of respiration. Krill depth behaviour was most sensitive to changes in mortality, while the accumulated energy was most sensitive to changes in food availability.

DISCUSSION

DVM at South Georgia

Most krill in the model exhibited a classic DVM, migrating downwards during the day and upwards during the night, with some exceptions. Throughout the simulations of high and low food concentrations and for both small and large individuals, krill occupied the deep layers during the day. However, depth at night was variable. On-shelf, with low food conditions, krill adopted a stable DVM in order to maximise food intake at night, but with high food conditions, most krill could be found in the deep water both day and night. Because of the high concentration of food on-shelf, small and large krill were still able to reach their target growth rates with this behaviour, which effectively minimised the risk of predation in this high-risk region. Off-shelf, there were also variations on DVM, but only for large krill. A proportion of large krill found off-shelf adopted deep high density swarms at night, more so when food availability was low. This suggests that large krill were able to maximise fitness by minimising predation risk and respiration, but also minimising food intake in deep high density swarms in this low food region. Small krill adopted DVM in the same region, perhaps because they were under more pressure to reach target growth rates, or because the cost of respiration in shallow low-density swarms did not outweigh the benefit of feeding there.

The occurrence of a classic DVM pattern has long been observed for both freshwater and oceanic zooplankton, and is believed to represent a trade-off between maximising food intake in the shallow water and minimising predation risk in the deep (Cuvier, 1817; De Robertis, 2002; Eiane and Parisi, 2001; Russell, 1927). However, a variety of patterns in vertical migration have been reported for krill (Everson, 1983; Godlewski, 1996; Hays, 2003; Hernandez-Leon et al., 2001; Loeb and Shulenberger, 1987). Reverse migration (i.e. upward migration during the day and deeper at night) is a type of migration that is usually associated with high levels of either invertebrate predators that use tactile stimuli or predators that feed at the surface (Hays, 2003; Verity and Smetacek, 1996). This type of migration has been observed at South Georgia (Godlewski, 1996; Kalinowski, 1978). Other authors have reported that the depth and migrational amplitude of DVM changes in proportion to the concentration of chlorophyll in an area (Godlewski, 1996). This was apparent in the model, with depth increasing in simulations of higher food concentration. The pattern may arise through greater dispersion through the water column in order to feed (Burrows and Tarling, 2004). This may result from midnight sinking, where krill sink upon satiation, and krill with different stomach sizes and feeding rates sink at different times (Emsley et al., 2005; Tarling et al., 2000; Tarling and Johnson, 2006). Furthermore, size- and sex-dependent DVM may be widespread in zooplankton (De Robertis, 2002; Godlewski, 1996; Tarling, 2003). When predation is high, such as close to an island, there is evidence that smaller animals will enter riskier shallow waters at higher light intensities than larger animals (De Robertis, 2002). This may be because they are less visible to visual predators or because they have a shorter starvation tolerance than larger individuals (De Robertis, 2002). I predict differences in the pattern of DVM due to

differences in the balance between maximising energy and minimising mortality. Testing this trend requires an accurate estimation of how mortality changes with distance from an island.

Schooling behaviour

Diel differences in swarming

The model predicted deep high-density swarms during the day for krill in nearly all simulations, and shallow low-density swarms at night in most simulations. Deep high-density swarms occurred during the day because krill could save energy and minimise high predation rates at this time with this behaviour. The consistent prediction of deep, high-density swarms during the day could alternatively be an artefact of mortality between day and night or between swarms of differing densities being too extreme. It was noticeable that medium-density swarms were not predicted by the best estimate model. Low-density swarms occurred at night in the model simply because krill were coming to the surface to feed on higher concentrations of phytoplankton when mortality from diving predators was reduced. Dispersing at this time maximised their food intake. The model also predicted deep high-density swarms at night for some krill, suggesting that predator avoidance in this instance was more important than energy intake; either because krill were easily reaching their target growth rates, or because the energetic reward in the shallow water was so low that a higher fitness could be obtained by saving energy and minimising mortality in a deep high-density swarm.

The density of swarms was most sensitive to changes in mortality relating to swarm density, highlighting the importance of obtaining quantitative evidence on how swarm density affects the risk of mortality in schooling krill.

While the occurrence of a classic DVM pattern is well known, there has been less work on diel patterns in swarming. There is some evidence that krill can be found in shallow and dispersed swarms at night, reforming into deep high-density swarms in the day (Croxall et al., 1985; Everson, 1982; Witek et al., 1981), but there is little experimental work to support this. Studies indicate that krill disperse in the shallow water to feed, sinking and forming swarms to save energy and decrease mortality risk at the point of satiation (Godlewska, 1996; Witek et al., 1981). However, as with DVM, care must be taken in assuming that diel patterns in aggregation are stable evolutionary strategies, because each situation is a unique trade-off between feeding and predator avoidance (Ritz, 1994). Schooling behaviour has been hard to study in the field because krill are open ocean animals, making direct observation and sampling difficult (Nicol, 2003). Acoustic observations can give estimates of krill density, but only in two dimensions, making it hard to determine the actual three-dimensional packing-density of a swarm. In addition, it is hard to study krill behaviour in the laboratory because in this situation krill do not form schools, but act as individuals (Hofmann et al., 2004; Strand and Hamner, 1990; Swadling et al., 2005). Even in a simple model such as this, completely different swarm densities could be found for different krill in the same area due to slight changes in the trade-off balance between feeding and predator avoidance. It is important to understand factors affecting swarm density because, like DVM, this is a major aspect of krill behaviour and affects krill availability to predators and fisheries. The model results predicted that mortality is the most important factor affecting swarm density.

Size dependent swarming behaviour

Small and large krill behaved differently in some zones during the day. On-shelf, a small proportion of small krill adopted deep low-density swarms during daylight hours, but all large krill could be found in deep high-density swarms. The difference in behaviour on-shelf would suggest that the trade-off between energy intake and predator avoidance is slightly different for small and large krill. Off-shelf the difference could be seen in the night behaviour, where small krill were always in shallow, low density swarms, while large krill could be found in both deep high density and shallow low density swarms. High-density swarms at night occurred because large krill in the deep water could maximise their fitness from the energy saving combined with reduced mortality of being in a high-density swarm. Low-density swarms at night may have occurred where small krill were under more pressure than large krill to feed, or lost relatively less energy to respiration in this formation than large krill.

There are a number of explanations as to why krill of different sizes could be found in swarms of differing densities in the field. Firstly, small krill filter phytoplankton from the water at a much lower rate than large krill (Hofmann and Lascara, 2000), but their growth rates during January at South Georgia, relative to their size, are up to twice that of large krill (Atkinson et al., In Press), so perhaps there is a greater demand to be in lower density swarms where they can filter more efficiently. Secondly, large krill in the model could potentially maximise fitness by the energetic saving combined with reduced mortality of being in a high-density swarm, compared to the increased respiration and mortality associated with feeding in the shallow water in a low-density swarm, particularly in low food conditions. This is based on the idea that krill can save energy in higher density swarms due to hydrodynamic effects (Ritz, 2000; Ritz et al.,

2003). Indeed, there is evidence that krill sink and reform into schools after feeding in the shallow waters (Godlewska, 1996; Tarling et al., 2000), and that in the deep water they swim slower in school formation (Zhou and Dorland, 2004), which would imply a further energetic saving (Swadling et al., 2005). It must be noted that krill in the model could not save energy by swimming slower because respiration was not dependent on swimming speed. Finally, in the field, differences in swarm density could be attributed to the idea that small krill face a lower risk of mortality from diving predators that may select large krill preferentially. In a study at South Georgia, the krill taken by macaroni penguins was significantly different from those caught by nets, with small krill absent from stomach samples (Hill et al., 1996). This result was supported by a broader study on predators at South Georgia, where diving predators preferred adult krill (Reid et al., 1996). This last factor needs to be tested by including a size-dependent mortality function in the model.

These findings provide a testable hypothesis with which to re-examine nets and acoustic data to validate or disprove the prediction that large krill form denser swarms than small krill off-shelf at night, and on-shelf during the day.

Advection

Krill influencing their position

Krill in the model were able to increase or decrease their likelihood of staying in an area by changing their swimming speed and turn rate. However, there was little evidence that krill altered their depth to change their location. Areas that ended up with the highest concentrations of krill were areas where krill chose to swim slowly and turn more often. Areas that ended up with the lowest concentrations of krill were areas

where krill chose to swim more quickly and turn less often. The final concentration of krill in an area was most sensitive to changes in mortality relating to distance from the island, and abundance of phytoplankton in the model. The highest overall concentration of krill was at the shelf-break for all sizes and simulations of varying food level.

High concentrations of krill have been associated with areas of water turbulence, often coinciding with high phytoplankton concentrations, such as eddies, fronts and at the shelf-break (Godlewska, 1996; Hunt et al., 1992; Trathan et al., 2003; Witek et al., 1981). In addition, there is a general tendency for higher concentrations of krill on-shelf than off-shelf, (Hunt et al., 1992; Siegel, 2000a) although this is not always the case. Some researchers believe krill are passively advected to certain regions where they concentrate (Fach et al., 2002; Hofmann and Lascara, 2000), but the degree to which processes other than advective transport influence observed Antarctic krill distribution are relatively unknown (Hofmann and Murphy, 2004). Some authors suggest that krill as a swarm can sense gradients in phytoplankton and temperature, and can therefore locate and move to more favourable areas of higher phytoplankton concentration (Grunbaum, 1998; Hofmann et al., 2004). In this way krill seem to know where they are going, as they act as 'super' organisms.

On a smaller scale, there has been some experimental work into the swimming behaviour of krill in favourable and unfavourable areas (McGehee and Jaffe, 1996; Price, 1989), but little work to combine how this behaviour would affect the distribution of swimming krill in combination with currents in a given area (Zhou and Dorland, 2004). Vertical migration of krill can also affect their horizontal distribution where surface and deep currents are significantly different (Hofmann and Murphy, 2004),

which has been shown for other species (Emsley et al., 2005; Hardy, 1936; Rogers, 1940; Schultz et al., 2000), although some authors suggest the krill are unlikely to use this to change their position (Hays, 2003). Depth choice was slightly influenced by the removal or addition of advection in the model, but most sensitive to mortality. This could be partly due to the fact that currents to the north of South Georgia in January are slow, 3 cm s^{-1} (Webb and de Cuevas, 1998; Webb and de Cuevas, 2003), in comparison to the potential swimming speed of krill, up to 15 cm s^{-1} (Kils, 1981). In addition, respiration did not increase with swimming speed in the model, so krill could choose a faster swimming speed as a way of dispersing from an unfavourable area with no additional cost to fitness. This is perhaps unrealistic because there is recent evidence that respiration increases linearly with swimming speed when krill swim faster than 5 cm s^{-1} (Swadling et al., 2005), contradicting previous suggestions that respiration would not change significantly with swimming speed (Kils, 1981). The interesting result is that krill in the model were able to increase their concentration in favourable areas without knowing where they were going, sensing gradients, or without the currents directing them to these areas, but simply by having a lower swimming speed with a higher turn rate in favourable areas, and higher swimming speed with a lower turn rate in unfavourable areas.

Size dependent trends in krill concentration

Running the model with low levels of phytoplankton resulted in large krill being around four times more concentrated than small krill on-shelf. The difference in concentration for small and large krill in this situation was due to a difference in swimming behaviour, with all large krill choosing a swimming behaviour that would maximise the probability of staying on-shelf, and a proportion of small krill choosing a behaviour that increased

dispersal from the region. Behind the different choice in swimming behaviour was a difference in the trade-off between mortality and feeding for small and large krill. In a low phytoplankton year, there was not sufficient food in any of the zones for large krill to meet their growth rates, but the concentration of phytoplankton was highest on-shelf. Here, both mortality and phytoplankton abundance were higher than any other region, but large krill could reduce mortality rates by adopting a stable DVM pattern, and maximising food intake at night by being dispersed. Small krill could still reach their growth rates on-shelf, but could maximise fitness at the shelf-break region where phytoplankton availability was not as high as on-shelf, but predation was reduced in comparison.

Differences in the behaviour of small and large krill have been observed regarding the vertical distribution of krill in the water column (Godlewska, 1996), but there has been less work on size differences in horizontal distribution. In general, smaller krill are found to the east of South Georgia, and larger krill to the west. This is most likely because young krill are transported from the Antarctic Peninsula and grow on their journey, which takes them first to the eastern end of South Georgia and then along the northern side to the west (Atkinson et al., 2001; Fach et al., 2002). This assumes that krill are passive particles that do not affect their own distribution. Other studies have looked at size differences in distribution, but on a larger scale and not specifically relating to bathymetry or South Georgia (Reid et al., 2004; Siegel et al., 2004; Witek et al., 1981). At the South Shetland Islands, krill in nets appeared to reflect the presence of larger krill offshore and smaller krill inshore (Reid et al., 2004). At the South Orkney Islands, small juvenile and immature krill occurred east of the islands, adult krill <50mm dominated the shelf areas of the Antarctic Peninsula and >50mm occurred

west of the islands (Siegel et al., 2004). Also in the region of the Antarctic Peninsula, one study found mainly gravid females in the Drake Passage, smaller krill in the Weddell Sea, and juvenile/adolescent krill on-shelf with males predominant (Witek et al., 1981). Differences in the distribution of small and large krill in the model were attributed a preference for different regions when food availability was low, due to different growth targets and energetic costs relating to size.

The model predicts that krill have a strong influence on their smaller scale distribution in terms of bathymetry around an island, and that small and large krill are not found in the same concentration on-shelf in a year of low phytoplankton availability. It is important to understand how a difference in krill size can affect distribution around a central foraging place because predators here are dependent on krill for their breeding success (Croxall et al., 1999). Modeling studies are useful in this area because little is known about variation in krill distribution around the Southern Ocean (Alonzo and Mangel, 2001). The patterns predicted here may well have a much wider application since krill are commonly found around on-shelf/off-shelf transition areas throughout the Southern Ocean (Atkinson et al., 2004).

Mortality

When mortality was included in the model, the growth rate of krill was greatly reduced, with a final energy level around a quarter of when mortality was excluded from the model. Such a large difference in energy levels can be explained in terms of krill behaviour. With mortality in the model, the depth and density of krill swarms was restricted, because the high mortality associated with shallow low-density swarms was too great a cost to fitness. Without mortality, krill were always in low-density shallow

swarms, effectively feeding in the shallow water day and night. This means that krill did not try to save energy in high-density swarms, even in the lowest phytoplankton conditions, suggesting that mortality is more important in the decision to form high-density swarms than energy saving. Indeed, the decision to swarm in the model was around twice as sensitive to changes in the mortality parameter than to changes in the energetic saving from being in a swarm.

Minimising mortality and maximising food intake is one of the most common ecological trade-offs (Ritz, 1994). Mortality is a driver for many of the behavioural decisions of Antarctic krill, from the small-scale immediate response of a swarm to a predator, to situations where the amplitude of DVM is varied in direct proportion to predator abundance and predation pressure in an area (Verity and Smetacek, 1996). Minimising mortality in these situations has costs in terms of reduced food intake, because both feeding and defence rely on motility (Verity and Smetacek, 1996), and avoiding predators often results in movement to areas with a lower food concentration. The formation of a swarm is a good example of this trade off, with benefits of reduced mortality due to increased vigilance and group defence tactics, and costs including reduced food intake due to intraspecific competition for food (Hamner and Hamner, 2000; Morris et al., 1983; Ritz, 1994; Ritz, 2000). In addition, there may be a further benefit to swarming in terms of reduced energy usage from hydrodynamic effects (Ritz, 2000). Although the relative importance of each of these factors is unknown, results from the model strongly suggest that mortality is the most important factor driving the decision to swarm.

Phytoplankton concentration

Phytoplankton availability was an important forcing factor in the model, particularly in terms of krill growth where it had more of an effect than changes in mortality. The relationship between phytoplankton availability and the final energy level of krill was non-linear. Phytoplankton over all of the zones increased on average by a factor of 1.6 from a low food to a high food year, while the final energy level of krill increased by a factor of 4.

Krill are believed to rely on phytoplankton as their primary food for spring and summer (Ross et al., 2000)(Alonzo and Mangel, 2001; Hofmann and Lascara, 2000; Ikeda and Dixon, 1982; Nicol, 2000; Nicol et al., 1992; Quetin et al., 1994), and are shown to have higher growth rates at this time of year in comparison to winter, when phytoplankton is scarce and krill growth rates are slowed even to the point of shrinking (Ross et al., 2000). Although phytoplankton availability is known to affect krill growth rates, the relationship is complicated for a number of reasons. Firstly, even though krill are generally thought to be mostly herbivorous during the summer months (Price et al., 1988; Ross et al., 2000), they are omnivorous at other times or in certain locations (Atkinson and Snyder, 1997). Large krill in particular have been shown to rely on the additional food source of copepods, dinoflagellates and ciliates even in phytoplankton dominated waters (Fach et al., 2002). Small krill may not prey upon on copepods to the same extent because of difficulties in capture and ingestion (Fach et al., 2002). Secondly, there is evidence that krill ingestion of phytoplankton reaches a maximum at intermediate levels of phytoplankton, declining at low cell concentrations and above a critical concentration (Boyd et al., 1984; Quetin and Ross, 1985), while other authors report a more simple linear increase in ingestion with increasing phytoplankton

concentration (Antezana et al., 1982; Kato et al., 1982; Price et al., 1988). The discrepancies between reported functional responses could be due to differences in the size and type of phytoplankton particles and the range of concentrations used, particularly the critical maximum where ingestion levels out, because these high concentrations are uncommon in the field (Holm-Hansen and Huntley, 1984; Price et al., 1988; Ross et al., 2000). Finally, phytoplankton is notoriously patchy over space and time (Fach et al., 2002). At South Georgia very little is known about horizontal patchiness of phytoplankton (Atkinson and Snyder, 1997), although it is believed to be patchy over scales of 10 to 20km (Atkinson et al., 2001). Despite the complicated relationship between phytoplankton availability and krill growth, phytoplankton clearly had the greatest effect on krill growth in the model.

Growth rates

With high phytoplankton availability, all krill reached their target in terms of specified growth rates, more than tripling the target at the shelf-break region. The target growth rate was that which krill in the model had to reach to gain a fitness reward at the end of the model time period, based on recorded daily growth rates for small and large krill at South Georgia in the summer (Atkinson et al., In Press). In a year of low phytoplankton availability, only small krill on-shelf and at the shelf-break region could reach their target growth rates, but all krill maintained a positive energy balance. Large krill may have struggled to reach their growth rates more than small krill because of the relatively high cost of respiration for large krill. Overall, in good food conditions, large krill had higher energy levels than small krill, and in bad food conditions, small krill had higher energy levels than large krill.

Growth rates are dependent on the correct parameterisation of energy input and output. In calculating the balance in energy, respiration rates for krill are mostly carried out on individual animals (Ritz et al., 2001). This can potentially lead to an overestimation because krill may save energy in a swarm, although the parameterisation of this is still poorly understood (Swadling et al., 2005). Alternatively, energetic input may have been too low in the model. Krill are omnivorous (Atkinson and Snyder, 1997; Price et al., 1988), and although many authors suggest that phytoplankton is their primary source of food during the spring and summer (Ross et al., 2000), it is likely that they supplement their diet from alternative sources. For larger krill in particular, additional food sources such as copepods, dinoflagellates and ciliates have been shown to contribute significantly to carbon intake, even in phytoplankton dominated waters (Fach et al., 2002), with ingestion rate of copepods found to be independent of phytoplankton concentration (Price et al., 1988). In another study, zooplankton fragments comprised around one fifth of identifiable items in the guts of South Georgia krill during the summer of 1994 (Atkinson and Snyder, 1997). There is evidence that the reliance on copepods is more pronounced outside of bloom periods (Atkinson et al., 1999), which could be similar to the conditions simulated in the model with low phytoplankton availability. Overall, with the best estimate parameterisation of the model, some small and all large krill could not reach their target growth rate with a low food availability.

At the shelf-break

The behaviour of krill at the shelf-break region in model simulations of low and high phytoplankton availability made them more vulnerable to predation than in other regions. Krill chose a swimming behaviour that resulted in a large increase in concentration in the region, at least five times higher than any other region, making

them more available to predators. Krill adopted this behaviour as a result of the favourable balance between mortality and food intake in this region, particularly in high food conditions. The resulting large difference between krill concentration at the shelf-break and in other regions may partly be the result of the difference in mortality between zones being too extreme.

In addition, with high food conditions, the model predicted low-density swarms day and night for all krill at the shelf-break, again increasing their vulnerability to predators. This behaviour does not occur in low food conditions perhaps because the cost of increased mortality and respiration from adopting low-density deep swarms outweighed the benefit of maximising feeding in the deep water. However, rather than swarming the model predicts that krill perform DVM in this environment as their main strategy of reducing predation. This finding stresses the importance of knowing both depth and density of krill with changing conditions, because both are equally important in terms of their availability to predators and also to the krill fishery.

The shelf-break region is believed to have a higher availability of krill because of observations that marine birds and mammals are often found at high concentrations here (Brown, 1980), and krill fisheries target the shelf-break region at South Georgia (Trathan et al., 1998). However, the reasons behind this trend are not well understood. Some authors suggest that krill end up in areas of water turbulence because of currents (Witek et al., 1981). Here I predict that krill accumulate in this region to exploit the higher primary productivity at a lower risk than feeding on-shelf. To achieve this, krill only have to exhibit a simple turning response and change of swimming speed to food availability.

Changing the terminal reward

The model predicts that krill adopt a more risky behaviour if fitness is accrued each time the krill eats rather than accrued at the end as a terminal reward. The least risky behaviour is predicted when the terminal reward is linear with no threshold, and a behaviour of moderate risk is predicted when krill have a target amount of energy to accumulate in order to obtain a fitness reward. Changing the terminal reward did not have a large effect on krill behaviour or the resulting energy levels and concentration in each of the zones. The model with terminal reward 1 was that used in best estimate parameterisation, predicting a medium level of both risk for krill behaviour and resulting energy levels. It is likely that krill with terminal reward 2 adopted the most risky behaviour because the fitness reward in this model was based more on the amount of energy the krill could ingest each time step, with less of a consideration towards mortality. The least risky behaviour was predicted by terminal reward 3 when krill did not need to reach a threshold energy level in order to obtain a fitness reward, and therefore did not need to work as hard particularly in challenging conditions, for example low food availability and high predation.

The specification of the terminal fitness reward is an important part of the model construction process. However, for iteroparous organisms that live to reproduce again in later life, the specification of the terminal reward is difficult (Clark and Mangel, 2000). Results from the current model indicate that changes in the terminal reward do not affect the overall qualitative predictions of the model, but do affect the magnitude of these predictions in certain scenarios, particularly when food availability was low.

SUMMARY OF FINDINGS

- DVM was common but not always exhibited by krill in the model. Both small and large krill did not migrate vertically on-shelf and large krill failed to do so off-shelf.
- Krill in the model were mostly in shallow low-density swarms at night and high-density deep swarms during the day. The density of swarm was more sensitive to changes in mortality than changes in food concentration.
- The model predicted that large krill could be found in denser swarms on-shelf than small krill, due to the trade-off between minimising mortality and maximising energy intake.
- Krill were able to increase their overall concentration in favourable areas without knowing where they were going, sensing gradients, or without the currents directing them to these areas, but simply by having a lower swimming speed with a higher turn rate in favourable areas, and higher swimming speed with a lower turn rate in unfavourable areas.
- Overall concentration of krill was highest at the shelf-break, even though the growth rate of large krill was lower here than on-shelf in low food conditions, highlighting the importance of the balance between mortality risk and food availability.
- Including mortality in the model greatly reduced growth rates. In addition, changes in mortality had the greatest effect on depth and density of swarms.
- The final energy level of krill was most sensitive to changes in the availability of phytoplankton.

- Both phytoplankton availability and changes in mortality had an effect on krill distribution.
- With low levels of phytoplankton availability in the model, some small krill and all large krill did not reach their target growth rates for the summer.
- Krill were more available to predators at the shelf-break, particularly in years of high phytoplankton.

FUTURE VALIDATION

The following experiments would be recommended for testing the predictions made with the model in this chapter:

- Using nets and acoustics to examine the depth and density of swarms against the size of krill in areas and years of interest, particularly to determine if krill are deeper and denser on-shelf and more dispersed at the shelf-break with high food conditions compared to low.
- Examining acoustic data to see if krill concentration is highest at the shelf-break in general. In addition, to determine if the distribution of small and large krill on-shelf is different in years of low phytoplankton availability.
- Compare actual krill concentration to that predicted by passive flow particle models to determine if krill can potentially affect their distribution by changing swimming speed and turn rate.
- Determine if the overall energy level of krill is higher in a high phytoplankton year. If not then expect that alternative food may play a part. Alternatively, examine

these data to see if krill do not reach their average growth rates in years of poor food availability.

4.

Optimal behaviour responses of krill during advection across the Scotia Sea

INTRODUCTION

Over half of the Southern Ocean krill stocks are concentrated into the Scotia Sea, an area in the southwestern Atlantic sector of the Southern Ocean that represents <25 % of the total habitable area available to this species (Atkinson et al., 2004; Constable et al., 2003; Marr, 1962; Nicol, 2000; Siegel, 2000). Along with high krill biomass, there are a number of other factors that contribute to the unique characteristics of this region. Here, two major components of Southern Ocean circulation meet; the Antarctic Circumpolar Current (ACC) and the Weddell Gyre (Deacon and Moorey, 1975; Hofmann et al., 1998), the properties of which can have major effects on krill distribution and transport. A large number of land-based higher predators that depend on krill breed throughout the Scotia Sea (Croxall et al., 1988; Reid et al., 2002). It is also the main location of the international krill fishery (Everson and Goss, 1991; Murphy et al., 2004; Nicol and Foster, 2003; Siegel, 2005). The Scotia Sea is a notably variable environment, where patchiness in chlorophyll over space and time, an interannually variable and seasonal sea-ice extent, and large-scale effects such as El Niño and the Antarctic Circumpolar Wave have a profound influence on krill population dynamics (Atkinson et al., 2004; Daly and Macaulay, 1991; Fraser and Hofmann, 2003; Meredith et al., 2005; Murphy et al., 2004; Siegel, 2005).

Within the Scotia Sea, adult krill occur from the Antarctic Peninsula to South Georgia, although both abundance and range vary according to the extent of sea-ice and frontal currents in the ACC (Atkinson et al., 2004; Mackintosh, 1973; Marr, 1962; Murphy et al., 2004). Krill in the south of the Scotia Sea are at their maximum abundance during the austral summer after the retreat of the sea-ice (Siegel, 2000). This time of year is also when a number of krill are believed to undergo a significant journey via passive transport from the spawning grounds close to the Antarctic Peninsula (Marr, 1962) to South Georgia (Murphy et al., 2004).

It has long been suspected that krill at South Georgia are not self-sustaining and there is evidence to suggest that these krill originate from the Antarctic Peninsula (Fach et al., 2002; Hofmann et al., 1998; Mackintosh, 1973; Marr, 1962; Murphy et al., 1998), or possibly from the Weddell Sea via the Weddell Gyre (Atkinson et al., 2001; Hofmann et al., 1998; Siegel, 2005). This has been indicated by both modelling studies and drifter tracks with the journey from the Antarctic Peninsula to South Georgia taking from between 140 to 160 days (Fach et al., 2002; Murphy et al., 2004; Thorpe et al., 2004).

Previous work has focussed on possible krill pathways across the Scotia Sea using physical models of currents and particle-tracking schemes (Hofmann et al., 1998; Hofmann and Murphy, 2004; Murphy et al., 2004; Thorpe et al., 2004). Some of the models also consider the difference that krill behaviour, in terms of depth choice, may have on possible transport pathways (Murphy et al., 2004). Further work has combined the physical with biological models, in an attempt to simulate krill growth under plausible conditions for the journey (Fach et al., 2002; Hofmann and Lascara, 2000).

However, no studies so far have examined both the behavioural and growth response of krill to the changing conditions of the journey, and this is where an SDP model provides a different and useful way of looking at the situation. In addition, advancements in Geoinformation technology make it now possible to extract environmental and geophysical data along hypothetical tracks, so enabling the influence of environmental variability in both space and time to be considered. Such information includes food proxies (SeaWiFS/MODIS derived Chl a), sea surface temperature and nearest distance to predator colonies.

Summer in the Scotia Sea is characterised by a low chlorophyll abundance that is patchy over a range of scales (Atkinson et al., 2001; Daly and Macaulay, 1991; Korb et al., In press; Okudo, 1978; Weber et al., 1986; Whitehouse et al., 1993). These conditions are characteristic of the Southern Ocean, where nutrients can be found in high concentrations but chlorophyll is paradoxically low (Korb et al., 2004). Many authors have suggested that krill in low chlorophyll regions such as this may also need to consume a substantial proportion of heterotrophic food in order to meet energy demands (Atkinson et al., In Press; Croxall et al., 1988; Fach et al., 2002; Holm-Hansen and Huntley, 1984; Pakhomov et al., 1997; Perissinotto et al., 1997). Krill are also under pressure from a land-based predator abundance that reaches its peak at this time of year as the breeding season commences (Croxall et al., 1988). Krill near such colonies will encounter high mortality (Murphy, 1995; Murphy and Reid, 2001; Reid et al., 2004). Outside of the range of colonies, it is likely that other visual predators, such as pelagic fish (Barrera-Oro, 2002; Lancraft et al., 2004) and tactile predators such as chaetognaths and jellyfish (Hamner and Hamner, 2000; Hays, 2003) have a greater effect on the predation rate on krill. These predators are also present within the range of

colonies but are likely to have less of an impact on krill than the land-based predators that are at a much higher abundance. Krill mortality in the Scotia Sea is therefore potentially high but variable, as krill pass at different distances from colonies of predators (Murphy and Reid, 2001). Due to the spatial variability in both food and mortality, conditions along the journey from the Antarctic Peninsula to South Georgia have the potential to change quickly. This is particularly true for open ocean regions in the Scotia Sea, where current speeds are generally high (Hofmann et al., 1998; Murphy et al., 2004).

Krill can respond to a changing landscape of predation risk and food availability by migrating vertically in the water column (Russell, 1927). Acoustic surveys report a wide range of vertical migratory patterns associated with krill that may be related to a number of factors including food abundance and distribution, physiological condition, age, predation risk and hydrographic conditions (Eiane and Parisi, 2001; Everson, 1983; Godlewska, 1996; Kalinowski, 1978; Loeb and Shulenberger, 1987; Tarling et al., 2000). Despite strong evidence for DVM in the Southern Ocean, there are few direct studies on the diel depth of krill across the Scotia Sea region, with most work focussed on the general abundance, distribution and growth of krill. Krill appear to respond to changes in their environment on relatively short time-scales (Ross et al., 2000), but whether krill respond in terms of DVM to conditions that are changing daily or weekly is unknown. DVM is a behavioural strategy, ultimately under the control of natural selection, however there is little idea about whether the DVM response can also change at a smaller scale, in response to local factors. Looking at krill behavioural depth response in relation to predator colonies and food patchiness is a good way to determine how stable a strategy such as DVM is when faced with constantly changing conditions.

Such a study also gives an opportunity to look at the relative importance of predation risk and food intake in the decision to migrate in the water column under challenging conditions.

Another behavioural response available to krill when faced with varying food availability and predation risk is swarming and dispersing (Daly and Macaulay, 1991; Siegel, 2005). Increased swarm density is believed to result in lower predation risk, due to group avoidance strategies and increased vigilance (O'Brien, 1987; Ritz, 2000) but also lower food intake, due to intraspecific competition (Hamner and Hamner, 2000; Morris et al., 1983; Ritz, 2000). There has been some work into the density of krill in different regions of the Southern Ocean in relation to factors such as bathymetry (Trathan et al., 2003), although this was in two dimensions only. Trying to interpret the behaviour of krill from either two-dimensional echosounder records and from associated net tows is unlikely to provide real time understanding (Nicol, 2003). In addition, finding school density in the field is inherently difficult (Hamner and Hamner, 2000), while in the laboratory, krill show limited schooling behaviour (Hofmann et al., 2004; Strand and Hamner, 1990; Swadling, 2005). The use of a model to examine the dynamics of krill swarm density has not been attempted before, although its usefulness has been suggested (Ritz, 2002). Looking at the response of krill swarm density to a changing landscape of predation risk and food availability will potentially provide insight into how krill cope with the challenging conditions of the journey from the Antarctic Peninsula to South Georgia.

The ability of krill to deal with extreme variability is likely to have been part of the adaptive landscape in which the Southern Ocean ecosystem has developed, meaning

that resident species must have evolved to cope with not only the mean level of various forcing variables, but also the spectrum of variation (Murphy et al., 1998). Examining a section of the krill journey from the Antarctic Peninsula to South Georgia where conditions are challenging but highly variable may provide insight into the way that krill deal with variability on a range of scales. The strategy of krill in this area has further importance to the many land-based predators that rely on krill for their breeding success.

The SDP technique used in this chapter allows the prediction of an optimal behavioural policy in response to a particular set of probable conditions. The policy can then be used to predict krill responses, for example DVM and swarming behaviour, over a wide area with specific conditions. While SDP models were originally used to answer general questions, without using specific data, the application of the optimal policy to real conditions has been since used in a number of cases, for example modelling the avian migration of the western sandpiper *Calidris mauri* off the coast of California, affected by “favourable” wind conditions. The optimal policy was determined, then applied to the probability distributions of favourable wind conditions determined from meteorological data for each of the sites along the coast (Clark and Butler, 1999). There are other examples of this type of SDP modelling in Clark and Mangel (2000), specifically concerning the effects of climate change.

AIM

The aim of this chapter is to create an SDP model to examine the response of krill to conditions across the Scotia Sea during January, which is the height of summer and a key time for land-based predators. Krill in the model will respond to varying conditions

of phytoplankton availability, predator distribution, currents and time of day. The response of both small and large krill to these conditions will be measured in terms of their chosen depth and swarm density over time, and their resulting growth rates. Results will be presented in the context of a landscape where real conditions have been imposed.

METHODS

The model in this chapter composes an optimal policy, determined from average conditions across the Scotia Sea, applied to krill that are run along specific pathways from the Antarctic Peninsula across the Scotia Sea to South Georgia. The tracks of krill across the Scotia Sea were obtained from velocity outputs from a varying forced run of a global ocean circulation model (Parallel Ocean Climate Model; POCM_4C) and data from 12 mixed layer World Ocean Circulation Experiment (WOCE) drifters (Thorpe et al., 2004). The latitude and longitude positions from 30-day sections of 10 of these tracks, an equal number of model and drifter predictions, were extracted from the data. A time scale of 30 days was appropriate, because this chapter is primarily concerned with krill behaviour in January, the breeding season for land-based predators across the Scotia Sea (Figure 4.1). The model focuses on three regions: close to the Antarctic Peninsula (tracks 1, 3 and 6), in the open ocean region of the Scotia Sea (tracks 1, 2, 4 and 9), and near South Georgia (tracks 5, 8 and 10). These regions differ in terms of predator density and chlorophyll concentrations.

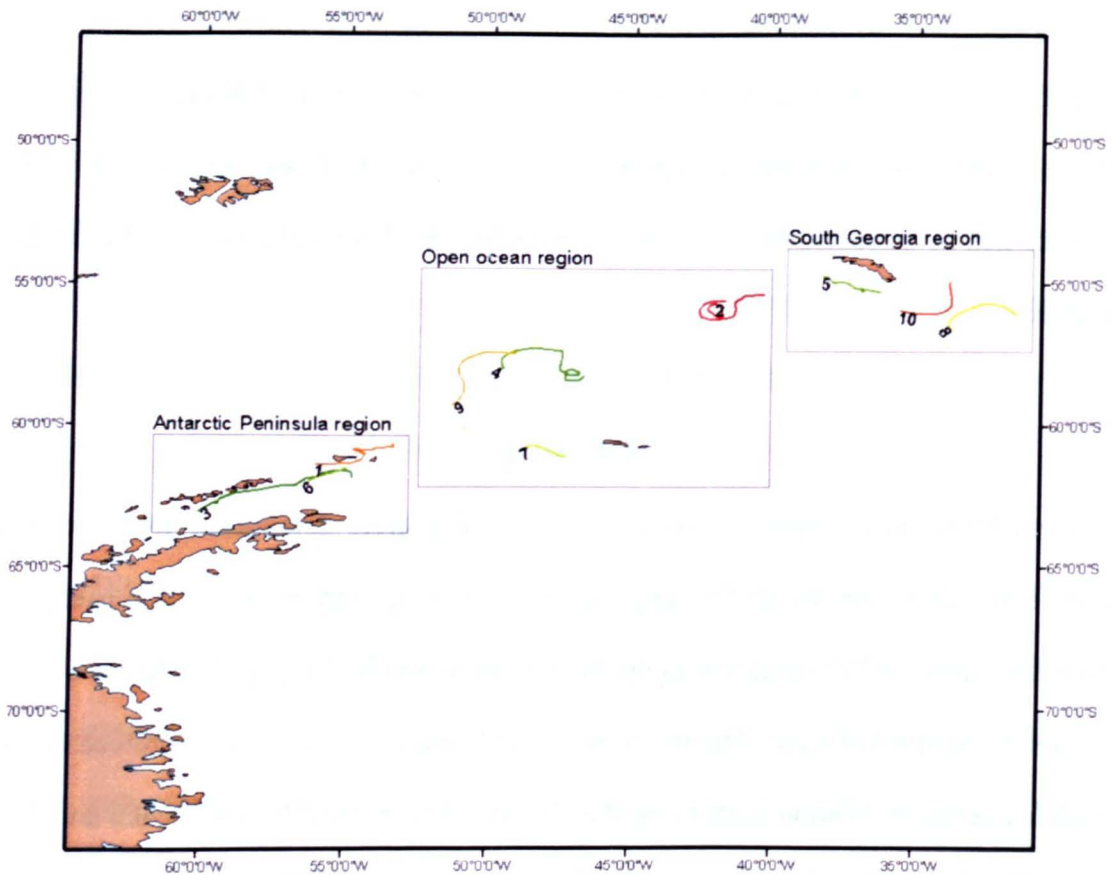


Figure 4.1. The predicted paths of krill across the Scotia Sea, for drifters and model predicted pathways (Thorpe et al., 2004). Although exact pathways vary, all generally move from southwest to northeast.

The model

The krill behavioural model used in this chapter is an SDP model, where krill respond to changing conditions across the Scotia Sea in terms of food availability, nearest distance to land and time of day. Krill make decisions based on their state, which is considered in terms of accumulated energy. At any time step, krill can choose one of two depths, shallow or deep, and three swarm densities, low, medium or high. The model was run separately for small and large krill, 30 and 50 mm total length (TL) respectively. Many parameters were required in the model (Table 4-1).

Parameters

Table 4-1. List of parameters used in the model.

Symbol	Parameter	Value	Unit
$F(e,z,m,t)$	Fitness is based on krill energy state, differs for small and large krill with zone and time	0 to 200	-
$F(T)$	Terminal fitness reward	0 to 200	-
i	Behavioural decisions made by individual krill at each time step	1 to 6	-
T	Final time step	360	6 h
t	Time step	6	h
L	Time of day	1 day or 2 night	-
d	Krill depth	1 shallow or 2 deep	-
s	Swarm density: low, medium and high	1, 2 and 3	-
z	Zone, nearest distance to shore	1 to 4 (Table 4-2)	-
e	Energy level	0 to 200	mg C
m	Total length (TL) of individual krill	small 30, large 50	mm
$WW(m)$	Wet weight, based on TL	small 209, large 1046	mg
$DW(m)$	Dry weight, based on TL	small 45, large 226	mg
$CW(m)$	Carbon weight, based on TL	small 19, large 101	mg C
$Chla(d)$	Concentration of chlorophyll a in the water, varies with depth	$0.13 < Chla < 2.64$	mg C m ⁻³
Cc	Carbon from chlorophyll	$Chla(d)*50$	mg C m ⁻³
Ch	Carbon from heterotrophic food	$Ch*0.09+ Hb$	mg C m ⁻³
Hb	Background heterotrophic carbon	20	mg C m ⁻³
$Cmax$	Maximum clearance rate	200	mg C m ⁻³
Cd	Carbon from detritus	$20.42+38.38*Chla(d)$	mg C m ⁻³
$Filt(DW)$	Filtration rate depends on DW	sm 0.006, large 0.012	mg C 6h ⁻¹
$Ffactor(s)$	Filtration reduced by factor with krill density	0.1 to 1	-
$Ingestion$	Assimilated ingested energy	$Filt(DW)*Chla(d)*0.8$	mg C (6 h) ⁻¹
$Resp(m,s)$	Respiration depends on krill size and swarm density	$0.06 < Resp < 0.3$	mg C (6 h) ⁻¹
$Rdensity(s)$	Respiration decreases by factor with density	0 to 0.2	-
$Rfactor(ing)$	Respiration increases by factor with ingestion	1 to 2	-
$MortL(t,d,s,z)$	Mortality risk near a colony, depends on time of day, depth, swarm density and zone	$1.6e-9 < Mort < 0.09$	Probability (6 h) ⁻¹
$MortO(t,d,s)$	Mortality risk in open ocean depends on time of day, depth, swarm density.	$1.6e-9 < Mort < 0.05$	Probability (6 h) ⁻¹

Most of these parameters are described as part of the model in Chapter 3. The main differences between the two models are in the parameterisation of food availability and mortality. However, the general model structure is also slightly different. These differences are described below, with a more general description of the present model.

The Fitness function F was linearly related to krill energy. Fitness increased with assimilated energy from ingestion, and decreased with respiration. Each time step, the krill tried to maximise fitness by maximising ingestion and minimising respiration costs, taking risks associated with different actions into account.

The terminal reward function $F(T)$ describes the fitness accrued at the final time step, dependent on the krill reaching a target energy level. The terminal reward differed from that used in the previous krill model (Chapter 3). In the present model, the fitness reward at the final time step was linearly related to accumulated energy. The possible fitness minimum and maximum was based on the minimum and maximum accumulated energy capacity of the krill, 0 to 200 mg C. In this model it was therefore possible to compare the observed growth rates of krill under the specified conditions in the Scotia Sea (Atkinson et al. In Press) to those predicted by the model when krill attempted to maximise fitness at each time step. The energy level r_m was calculated as the amount of assimilated carbon (minus respiration) that the krill accumulated over time.

Equation 4-1
$$F(T) = e \quad ; \quad 0 < e < e_{\max}$$

where e is the total accumulated carbon (assimilated carbon minus respiration) and e_{\max} is the maximum setting for accumulated energy, 200 mg C.

The model ran for a total of 360 time steps of 6 hours, approximately 3 months. However, results were taken from the middle month, from time step 121 to 240. This was to minimise artefacts that are inherent in this type of model; ‘stationarity’ is described in Chapter 3. Parameter estimates were again based on the month of January, when the main predators of krill, seals and penguins, remain close to land for the breeding season (Barlow et al., 2002; Barlow and Croxall, 2002; Green et al., 2002; Williams and Croxall, 1991). The time step of the model was 6 hours because the day length in the Scotia Sea during January is around 18 hours (www.exptech.com/sunrise.htm), thus dividing the day into three equal parts and the night into a single part.

Swarm density was parameterised as in the previous krill model (Chapter 3) and there were 4 zones in the model, characterised by nearest distance to shore (Table 4-2).

Table 4-2. Zone classification

Zone (z)	Distance from shore (x)
1	< 50 km
2	50 < x < 100 km
3	100 < x < 200 km
4	> 200 km

Energy level *e* was calculated as in the previous krill model (Chapter 3) with units of mg C. The size classes used for model runs were also the same as in Chapter 3, 30 and 50 mm representing small and large krill respectively. This is representative of the

main size classes present in the Scotia Sea during January (Atkinson et al., In Press; Tarling et al., 2006).

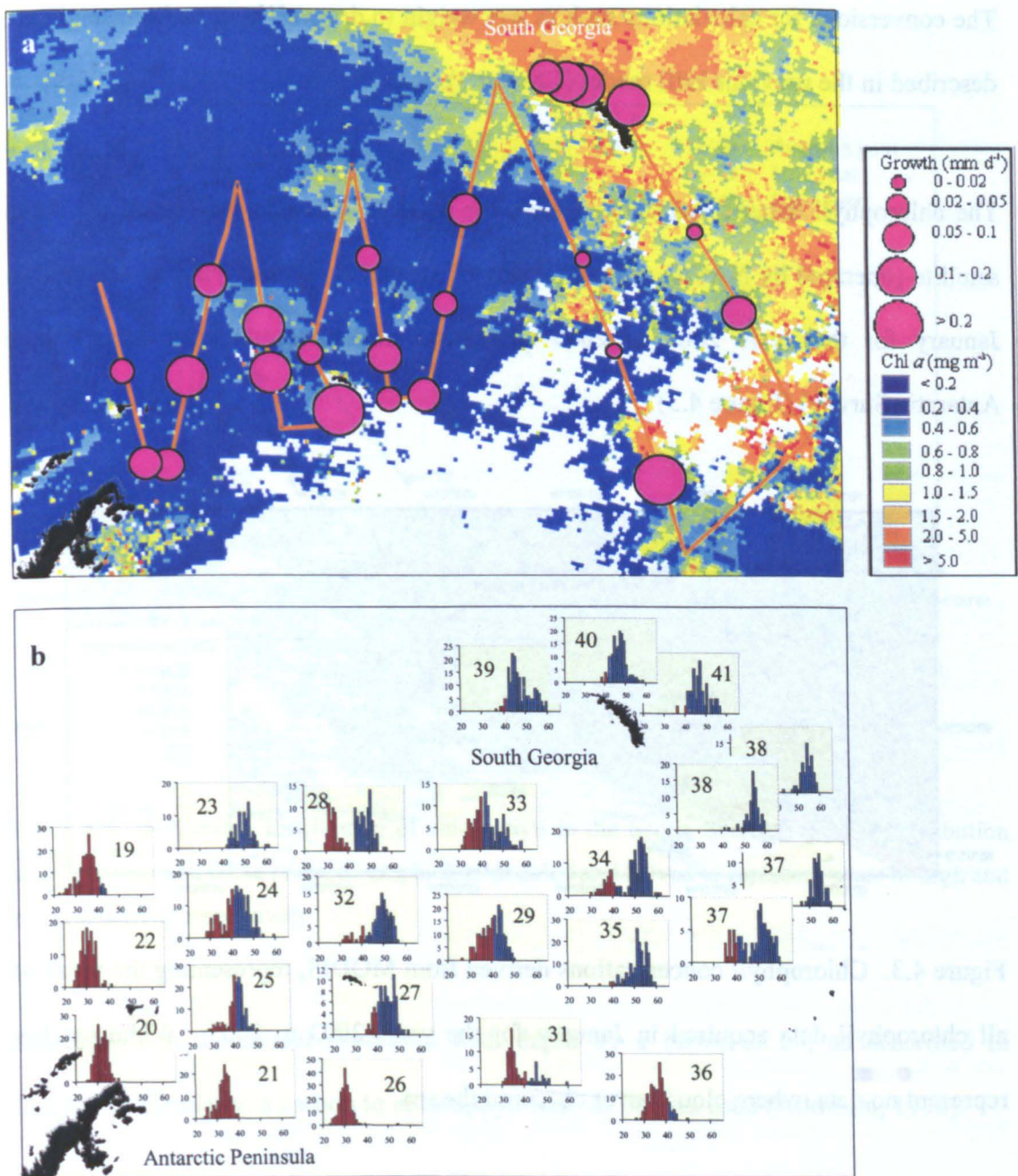


Figure 4.2. The (a) growth rates in mm d^{-1} and (b) size frequency distributions in mm of krill across the Scotia Sea at the various sampling sites during the 2003 survey, plotted against a composite SeaWiFS image from December 2002 to February 2003 (Atkinson *et al.*, In Press). In the top image, (a) the brown line shows the cruise track. In the bottom figure, (b) histograms are labelled with station numbers and are displaced slightly for clarity. Actual positions corresponding to these numbers are given in Tarling *et al.* (2006).

The conversions for calculations such as wet weight to dry weight or carbon weight are described in the previous krill model (Chapter 3).

The chlorophyll dataset was derived from the MODIS instrument on board the Aqua satellite (operated by NASA), giving a mean of all global chlorophyll data acquired in January for the years 2003 to 2005 (Andrew Fleming, unpublished data, British Antarctic Survey) (Figure 4.3).

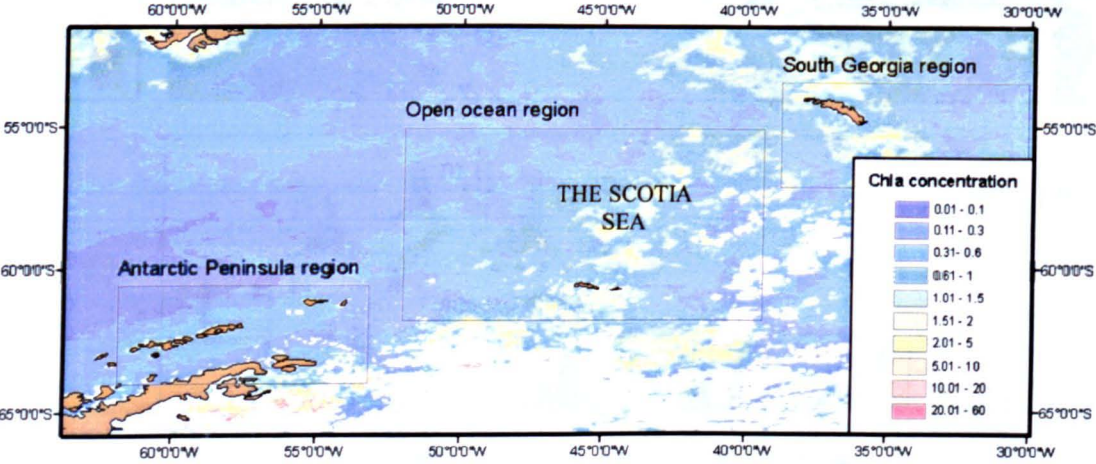


Figure 4.3. Chlorophyll concentrations derived from MODIS, representing the mean of all chlorophyll data acquired in January for the years 2003 to 2005. White patches represent no data, where cloud cover obscured the sea.

These values were assumed to describe an average year of chlorophyll abundance. In further sensitivity analyses, the values were doubled to simulate a year of high productivity, and halved to represent a year of low productivity. The probable distribution of different concentrations of chlorophyll was also extracted from this dataset (Figure 4.4).

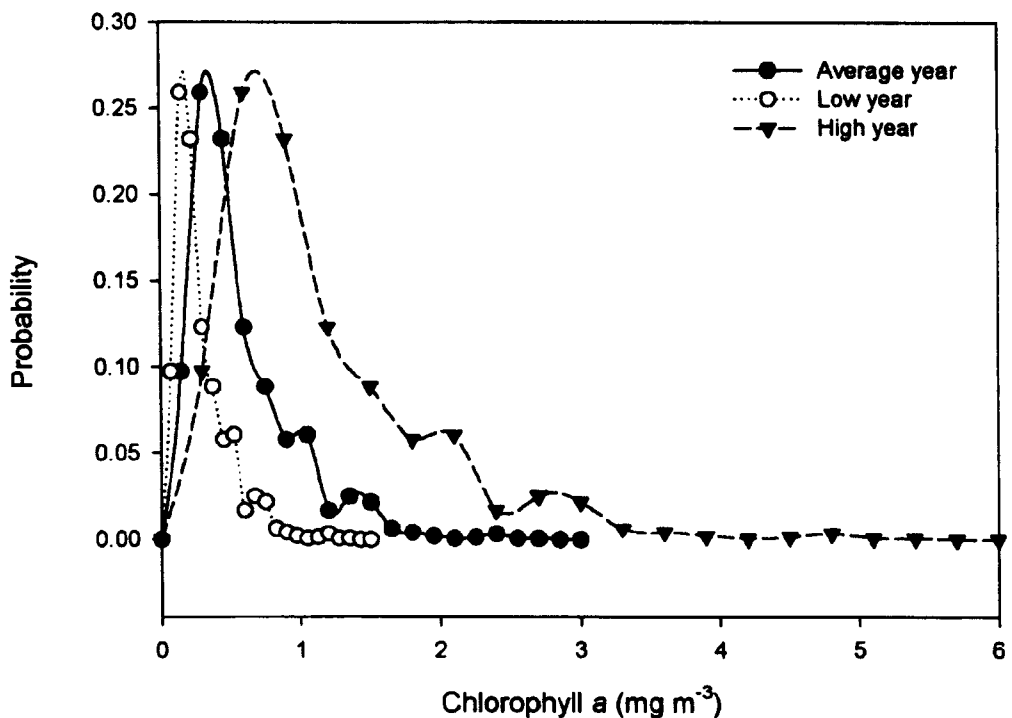


Figure 4.4. Probability distribution of chlorophyll in the Scotia Sea, the average distribution taken from data from the previous graph, then doubled and halved to represent years of high and low productivity respectively.

Chlorophyll in the model decreased with depth by a factor of 20, as described in Chapter 3. Similarly, a carbon to chlorophyll ratio of 50 was used (Atkinson, 1996).

Chlorophyll concentrations are typically low in the Scotia Sea (Korb et al., In press) meaning that krill need food other than pelagic phytoplankton to sustain growth rates observed in transport across the Scotia Sea from the Antarctic Peninsula to South Georgia (Fach et al., 2002). There have been a number of attempts to characterise other components of the diet of Antarctic krill, but the variety of approaches and diversity of functions reflect the difficulty of the task. For this chapter, the assumption is that there are 3 components to the diet: phytoplankton C_c , heterotrophs C_h and detritus C_d .

One option for parameterising the heterotrophic component C_h is to consider the total number of ciliates and protozoans (*no.ciliates*) in the water column. The numbers of these organisms has been related linearly to chlorophyll concentration by Atkinson et al. (In press), such that

$$\text{Equation 4-2} \quad \text{no.ciliates} = C_c \cdot 2.92 + 664$$

However, it is hard to convert the number of ciliates and protozoans into mg C m^{-3} because of difficulties in determining the volume of cells. There are many different species of ciliates and protozoans with differing cell volumes, and while some work has been done on freshwater ciliates and some seawater taxa (Menden-Deuer and Lessard, 2000), little is known of the carbon content of species in the Scotia Sea. Therefore, other than noting the linear relationship between numbers of ciliates and carbon from chlorophyll, I decided it was not practical to proceed in this way.

An alternative means of parameterising C_h can be extracted from by Atkinson and Snyder (1997) when comparing LHPR (long haul plankton recorder) samples to concurrent Chl *a* profiles. I extracted their datasets and derived the following equation.

$$\text{Equation 4-3} \quad C_h = C_c \cdot 0.09 + 60$$

where C_h is the carbon content from heterotrophic food and C_c the carbon content from chlorophyll *a*, units in mg C m^{-3} .

The important thing to note from the above equation is that it includes a background level of heterotrophic carbon in areas when chlorophyll is zero. However, because equation 1-3 was only estimated for the South Georgia situation, it was necessary to look for further references on heterotrophic food. Others have considered background heterotrophic food to be even lower, at 1 mg C with a maximum of around 70 mg C m⁻³ in the Scotia Sea (Fach, 2003; Fach et al., In press; Fach et al., 2002). For the current model, a background level was chosen that was intermediate with respect to these various studies (Equation 4-4). Other levels of background carbon were tested in the sensitivity analysis.

Equation 4-4
$$C_h = C_c \cdot 0.09 + 20$$

Carbon from detritus C_d , or the particulate organic carbon (POC) content in seawater, also contributed to krill food in the model. POC is the non-living component of seawater, and was parameterised from a study where measurements of POC and chlorophyll *a* concentrations were compared over several Antarctic cruises (Fach et al., 2002), giving the equation

Equation 4-5
$$C_d = 20.42 + 38.38 \cdot Chla(d)$$

where C_d in mg C m⁻³ was calculated from a varying chlorophyll *a* concentration $Chla(d)$ that varied with depth. Both the estimates for heterotrophic and detritus carbon are taken from surface measurements, so it is likely that the intercept, or background level of carbon may also change with depth. As there is no evidence on the relationship

between heterotrophic or detritus carbon with depth, the background level was divided by 20, the same as for Chl a C_c values.

Filtration rate was parameterised as in Chapter 3, decreasing with increasing swarm density. However this time a maximum clearance rate C_{max} was considered. Many previous studies have looked into the concentration of chlorophyll above which filtration and ingestion level out. Some authors report a simple linear increase in ingestion with increasing chlorophyll concentrations (Antezana et al., 1982; Price et al., 1988). Others report a decrease in clearance rate only above concentrations as high as 10 mg chl a m^{-3} (Boyd et al., 1984), suggesting, therefore, that krill do not become satiated under most field conditions. Further studies report maximum clearance rates at intermediate chlorophyll concentrations, declining below and above this (Quetin and Ross, 1985; Ross et al., 2000). For the model, a maximum clearance rate of 200mg C m^{-3} was used, based on Atkinson and Snyder (1997). This would mean individuals clearing an equivalent of 2 mg chl a m^{-3} along with background and heterotrophic food components.

Ingestion and respiration were calculated as in Chapter 3.

Mortality was parameterised in a slightly different way in this model, compared with the model in Chapter 3; due to the fact krill could be in a region that was out of the range of predator colonies, in the open ocean. Changes in mortality with depth and time of day were based on previous work (Aksnes and Giske, 1993; Fiksen and Giske, 1995; Tarling et al., 2000).

Table 4-3. List of parameters used to calculate mortality.

Symbol	Parameter	Value	Unit
er	Encounter rate	-	h^{-1}
M	Mortality	-	h^{-1}
β_y	Mortality rate for one year	-	yr^{-1}
β_l	Mortality close to an island	0.00014	$(6\ h)^{-1}$
β_o	Mortality in the open ocean	0.00006	$(6\ h)^{-1}$
v	Predator velocity (based on fish)	50 (Tarling et al., 2000)	$m\ h^{-1}$
N_l	Predator density near land	0.000194	$n\ m^{-3}$
N_o	Predator density open ocean	0.000487	$n\ m^{-3}$
dt	Time interval	1	h
θ	Field of view	0.5 (Tarling et al., 2000)	-
r	Visual range	-	m
z	Depth	0 to 60, 60 to 150	m
ψ_z	Chlorophyll concentration at depth z	0.6	$mg\ m^{-3}$
k_0	Extinction from non-chlorophyll	0.14 (Aksnes and Lie, 1990)	m^{-1}
K_z	Local diffuse attenuation coefficient	0.1387	m^{-1}
c_z	Local beam attenuation coefficient	$3 \times K_z$ (Fiksen and Giske, 1995)	m^{-1}
ρ	Light fraction lost at the surface	0.5 (Aksnes and Giske, 1993)	-
I_s	Irradiance at the surface	see (Tarling et al., 2000)	$\mu mol\ m^{-2}\ s^{-1}$
C_0	Inherent contrast of krill	0.5 (Aksnes and Giske, 1993)	-
A_{zp}	Krill cross-sectional area	0.0000126 (Tarling et al., 2000)	m^2
ΔS_e	Planktivore eye sensitivity	3.0×10^{-6} (Rosland and Giske, 1994)	$\mu mol\ m^{-2}\ s^{-1}$

Firstly, mortality was divided into two mean values, mortality close to land, $MortL(d,z)$, and mortality away from an island $MortO(d)$ (Table 4-1). The estimates for the instantaneous rate of natural mortality of krill vary from $\beta_y = 0.6$ to $\beta_y > 1\ yr^{-1}$ (Butterworth et al., 1994; Siegel and Kalinowski, 1994), where

Equation 4-6
$$M = 1 - e^{-\beta_y}$$

In a study on the South Georgia area, a higher β_y of 1.25 yr^{-1} gave the most accurate representation of local population structure using data from net hauls (Murphy and Reid, 2001). In the open ocean, away from predator colonies, Murphy and Reid (2001) estimated β_y to be between 0.5 and 0.6.

Mortality close to an island, $MortI(d,z)$, with $\beta_y = 1.25 \text{ yr}^{-1}$ was used in the model when distance to land was less than 150 km (zones 1 to 3), based on the maximum foraging range of major land-based krill predators, breeding seals and penguins (Murphy, 1995; Reid et al., 2004). Mortality in the open ocean, $MortO(d)$, with $\beta_y = 0.5 \text{ yr}^{-1}$ was used in the model when distance to shore was greater than 150 km (zone 4). These rates were adjusted to give a value for mortality over the 6 hour time step, with a corresponding mortality rate of $\beta_l = 0.00014 (6h)^{-1}$ close to land, and $\beta_o = 0.00006 (6h)^{-1}$ open ocean.

Mortality was affected by depth, distance from shore and time of day. In this model, visual predators were assumed to be the principal source of mortality for krill in the Scotia Sea, with predominantly land-based predators close to land, and fish in the open ocean. A method from Fiksen and Giske (1995) is used to adjust mortality according to depth and light intensity, requiring a number of parameters (Table 4-3).

The encounter rate, er , specifies the expectation that a krill will encounter a predator, and was calculated as a function of the visual range, r , speed, v , density of the predator, N , and the size of the prey (Eggers, 1977; Tarling et al., 2000), such that

Equation 4-7 $er = \pi r^2 v N d t$ (Tarling et al., 2000)

where θ is the field view of the fish and dt is the time interval, in this case 1 hour. It was assumed that each encounter, e , resulted in death of the krill, so that expectation of mortality, E , was calculated

Equation 4-8
$$M = 1 - \exp(-erd t) \quad (\text{Tarling et al., 2000})$$

Light is an important factor in the formulation of predation risk from planktivorous fish (Fiksen and Giske, 1995). The local diffuse attenuation coefficient K_z was calculated from the local chlorophyll concentration ψ_z , around 0.6 mg m^{-3} for the Scotia Sea, and extinction due to non-chlorophyll particles k_0 such that

Equation 4-9
$$K_z = k_0 + 0.054(\psi_z)^{0.667} + 0.0088\psi_z \quad (\text{Fiksen and Giske, 1995})$$

The predator visual range, r , was derived from a set of equations developed by Aknes and Giske (1993). This non-linear equation can be solved numerically for r using the Newton-Raphson iteration (Fiksen and Giske, 1995).

Equation 4-10
$$r^2 \exp(c_z r + zK) = \tilde{n} I_s |C_0| A_{zp} \Delta S_e^{-1}$$

where I_s is irradiance at the surface, ρ is the fraction of light lost at the surface (Table 4-3), diffuse attenuation K and beam attenuation c_z giving the turbidity, z is depth (here <60 m or 60 to 150m), A_{zp} is the krill cross-sectional area, C_0 is the krill inherent contrast, and planktivore eye sensitivity threshold for prey recognition ΔS_e . The beam attenuation coefficient was set at 3 times K_z (Fiksen and Giske, 1995).

The encounter rate er was solved for the above equations at every 5 m depth from 5 to 150 m for each hour of the day and night, using light intensity values parameterised for a latitude of $\sim 56^{\circ}\text{S}$ (Tarling et al., 2000), the average latitude of the study region. The encounter rate and corresponding average mortality M were averaged over 5 to 60 m, representing shallow krill, and 65 to 150 m for deep. Further, a stable DVM pattern was assumed, so krill mortality was taken to be the average of the mortality in shallow water at midnight and deep water at midday. Using this average value of M , fish/predator density was altered until the expectation of mortality M matched the average daily mortality for both open ocean ($M_o = 0.00138 \text{ d}^{-1}$) and near land ($M_l = 0.00347 \text{ d}^{-1}$). This resulted in a predator density of $N_o = 1.94 \times 10^{-4} \text{ m}^{-3}$ for open ocean and $N_l = 4.87 \times 10^{-4} \text{ m}^{-3}$ near land.

Now, in addition to the average mortalities, values for the encounter rate and corresponding expectation of mortality were calculated for the possible habitats of day deep, day shallow, night deep and night shallow using the newly calculated fish/predator density values. Firstly, the encounter rates were averaged over deep and shallow and divided into night and day. Then an average mortality for each of the habitats mentioned above was determined by assuming an initial number of 1000 krill and for each hour reducing the number surviving based on the encounter rate h^{-1} , for each combination of deep, shallow, day and night.

The average values for mortality, for both M_o and M_l , were divided by the mortality calculated for each of the possible habitats in depth and time to show the effect of habitat choice on mortality in terms of order of magnitude, for use in the log odds

function (Table 4-4). There was a difference between open-ocean and near-land as a result of different predator density and average mortality values. Depth choice only made a differences when krill chose a shallow habitat during the day (Table 4-4).

Table 4-4. Mortality is affected by 10^y, each of these components is considered in the mortality function for near colony populations.

Component	Near land	Open ocean
Day shallow	2.3	2.6
Day deep	-0.6	-0.6
Night shallow	0.5	0.5
Night deep	-4.3	-4.3
Swarm density 1	0.3	0.3
Swarm density 2	0	0
Swarm density 3	-0.3	-0.3
On shelf	0.3	-
Shelf break	0	-
Off shelf	-0.3	-

Table 4-5. Mortality probabilities, P' , for all the different combinations of depth (d), density (s), time of day (time) and zone (z), in probability of mortality h^{-1} . The second last two columns estimate how many krill would remain after a specified time interval, from an original number of 1 000 000, and the last column is the β value for mortality with a time step of 1 year.

d	s	z	x	x'	P'	Survive (6 h)	Survive yr	β_y
Day shallow	1	1	2.9	-1	0.091	909090	0	v. high
Day shallow	1	2	2.6	-1.3	0.048	952273	0	428.392
Day shallow	1	3	2.3	-1.6	0.025	975496	0	217.323
Day shallow	1	4	2.9	-1.3	0.048	952273	0	428.392
Night shallow	2	1	1.1	-2.8	0.002	998417	0.944	13.8727
Night shallow	2	2	0.8	-3.1	0.001	999206	953.326	6.9556
Night shallow	2	3	0.5	-3.4	0	999602	30600.93	3.4867
Night shallow	2	4	0.8	-3.4	0	999602	30600.93	3.4867
Day shallow	3	1	2.6	-1.3	0.048	952273	0	428.392
Day shallow	3	2	2.3	-1.6	0.025	975496	0	217.323
Day shallow	3	3	2	-1.9	0.012	987567	0	109.593
Day shallow	3	4	2.6	-1.6	0.025	975496	0	217.323
Night shallow	1	1	0.8	-3.1	0.001	999206	953.326	6.9556
Night shallow	1	2	0.5	-3.4	0	999602	30600.93	3.4867
Night shallow	1	3	0.2	-3.7	0	999800	174178.4	1.7477
Night shallow	1	4	0.5	-3.7	0	999800	174178.4	1.7477
Day shallow	2	1	2.3	-1.6	0.025	975496	0	217.323
Day shallow	2	2	2	-1.9	0.012	987567	0	109.593
Day shallow	2	3	1.7	-2.2	0.006	993729	0	55.0982
Day shallow	2	4	2.3	-1.9	0.012	987567	0	109.593
Night shallow	3	1	0.5	-3.4	0	999602	30600.93	3.4867
Night shallow	3	2	0.2	-3.7	0	999800	174178.4	1.7477
Night shallow	3	3	-0.1	-4	0	999900	416463.6	0.876
Night shallow	3	4	0.2	-4	0	999900	416463.6	0.876
Day deep	1	1	0	-3.9	0	999874	331957.2	1.1027
Day deep	1	2	-0.3	-4.2	0	999936	575393.5	0.5527
Day deep	1	3	-0.6	-4.5	0	999968	758046.1	0.277
Day deep	1	4	-0.3	-4.5	0	999968	758046.1	0.277
Night deep	2	1	-3.7	-7.6	0	999999	999780	0.0002
Night deep	2	2	-4	-7.9	0	999999	999889.7	0.0001
Night deep	2	3	-4.3	-8.2	0	999999	999944.7	0.0001
Night deep	2	4	-4	-8.2	0	999999	999944.7	0.0001
Day deep	3	1	-0.3	-4.2	0	999936	575393.5	0.5527
Day deep	3	2	-0.6	-4.5	0	999968	758046.1	0.277
Day deep	3	3	-0.9	-4.8	0	999984	870371.2	0.1388
Day deep	3	4	-0.6	-4.8	0	999984	870371.2	0.1388
Night deep	1	1	-4	-7.9	0	999999	999889.7	0.0001
Night deep	1	2	-4.3	-8.2	0	999999	999944.7	0.0001
Night deep	1	3	-4.6	-8.5	0	999999	999972.3	0
Night deep	1	4	-4.3	-8.5	0	999999	999972.3	0
Day deep	2	1	-0.6	-4.5	0	999968	758046.1	0.277
Day deep	2	2	-0.9	-4.8	0	999984	870371.2	0.1388
Day deep	2	3	-1.2	-5.1	0	999992	932782.8	0.0696
Day deep	2	4	-0.9	-5.1	0	999992	932782.8	0.0696
Night deep	3	1	-4.3	-8.2	0	999999	999944.7	0.0001
Night deep	3	2	-4.6	-8.5	0	999999	999972.3	0
Night deep	3	3	-4.9	-8.8	0	999999	999986.1	0
Night deep	3	4	-4.6	-8.8	0	999999	999986.1	0

Krill do not have a choice of swimming behaviour in this model, but are advected by the currents as assumed by the studies of Murphy *et al.* (2004) and Hofmann and Lascara (2000).

Running the model

The individual chooses from one of 6 decisions each time step; shallow or deep, and low, medium or high density. Each of these decisions will result in a different fitness value, worked out in terms of energy and mortality.

Table 4-6. All the behavioural decisions, i , in the model.

i	Depth (d)	Swarm density (s)
1	Shallow	Low
2	Shallow	Medium
3	Shallow	High
4	Deep	Low
5	Deep	Medium
6	Deep	High

Backward iteration

Fitness for each time step is the same as in the previous krill model (Chapter 3), according to

$$F(e, z, m, t) = \max_i (1 - \beta_i) F(e_i, z, m, t + 1)$$

Although size and zone are included in the dynamic programming equation, they are not dynamic state variable, but static state variable. The decision chosen at any time will not affect the state of zone or size in the next time step.

Energy at time $t+1$ resulting from any particular action is calculated by energy at time t plus assimilated energy from ingestion, minus the cost of respiration resulting from decision i .

Equation 4-11
$$e' = e + X_i - resp_i$$

where, X_i is the ingested food from of chlorophyll, heterotrophic food and detritus, with an assimilation of 0.8, such that

Equation 4-12
$$X_i = (C_c + C_h + C_d) \cdot 0.8$$

The dynamic programming algorithm was solved, creating an optimal policy for different values of energy, zone, and size, and for each time step backwards from the final time. This optimal policy was referred to in the forward iteration, as individual krill on the landscape had the opportunity to eat under some risk of predation.

Forward iteration

The model was run forward for only 1 small and 1 large krill per track using the conditions determined in the first section. Only one krill was run through the model because the conditions were determined from real data for each track, and the predicted behaviour will not change unless stochasticity is introduced. The model ran for 360 time steps, equivalent to 3 months. The krill chose the optimal decision, determined from the backward iteration, based on its state that is considered in terms of energy level, distance to land and size. The krill then had an opportunity to eat and respire at

this new depth and density. The new depth, density, zone and energy level were recorded for this time step, and the process was repeated until the final time T .

Model runs

The model was firstly run with best estimate parameterisation, and then a number of parameters were varied to test the robustness of the model (Table 4-7). Food availability was tested because conditions can vary considerably from year to year in the Scotia Sea (Korb et al., In press; Korb et al., 2004). The background level of heterotrophic carbon was tested because this was difficult to parameterise and poorly understood, except for the fact that krill can survive and grow on very low chlorophyll, most likely due to heterotrophic food (Atkinson et al. 2006). Effects of varying the form of the terminal reward were examined because this function can have a marked effect on the predictions of SDP models. Finally, the maximum clearance rate was tested in the sensitivity analysis, because again, this is hard to determine in the laboratory, and it is important to determine whether it may be an important parameter to measure with greater accuracy in the future.

Table 4-7. Parameters tested in the sensitivity analysis of the model.

Symbol	Parameter	Values tested	Units
$Chla(d)$	Phytoplankton availability	(average / 2), average, (average * 2)	-
C_h	Background heterotrophic carbon	20, 40, 60	mg C
$F(T)$	Terminal reward	target growth rates, fitness accrued, linear	-
C_{max}	Maximum clearance rate	200, 300, 400	mg C m ⁻³

These four parameters were each tested for 3 values each, with orthogonal combinations of all possible values ($3 \times 3 \times 3 \times 3 = 81$ simulations of the model for each of the 12 tracks and for small and large krill).

RESULTS

Results are firstly presented with the best estimate predictions of behaviour on a map of Scotia Sea, showing the changing conditions in terms of chlorophyll concentration and distance from shore for each of the tracks. Secondly, more specific graphs demonstrate the differences in conditions between the 3 regions, and give the corresponding results for the regions in terms of behaviour and accumulated energy. Finally, a number of graphs demonstrate the results of the sensitivity analysis. Although the model was run for 3 months, only the middle month is represented in the results section to minimise artefacts that are inherent in this type of model (see Chapter 3 for an explanation of stationarity).

Real conditions

The difference in conditions between the three regions of the model can clearly be seen by looking at the distribution of chlorophyll (Figure 4.5) and distances from shore (Figure 4.6), created by combining data from the tracks in each model region from the Scotia Sea. The concentration of chlorophyll is highest at South Georgia and lowest near the Antarctic Peninsula.

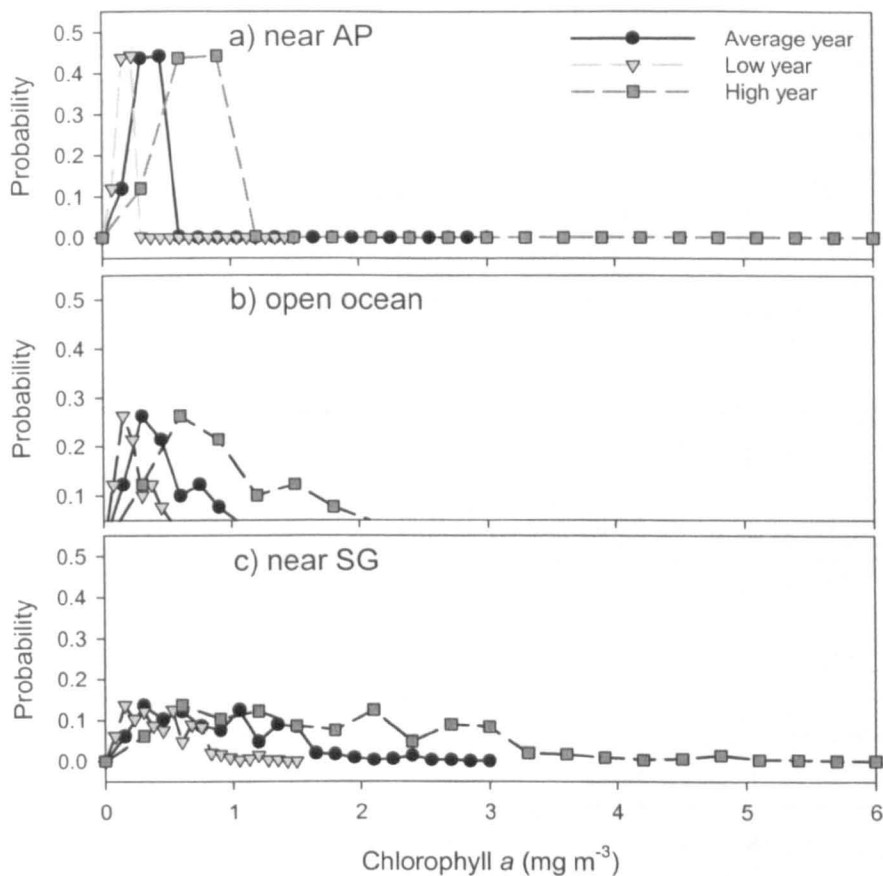


Figure 4.5. Chlorophyll conditions in each of the regions of the Scotia Sea with probable distribution of each discrete chlorophyll value (histogram).

Difference in nearest distance to shore for the combined track data clearly shows the differences between the three regions (Figure 4.6). Most of the tracks in the Antarctic Peninsula region come closer than 100 km to shore, with many under 50 km. Tracks in the open ocean region are spread much further, from 100 to 500 km from shore, while at South Georgia the distance from shore is intermediate, from 50 to 300 km.

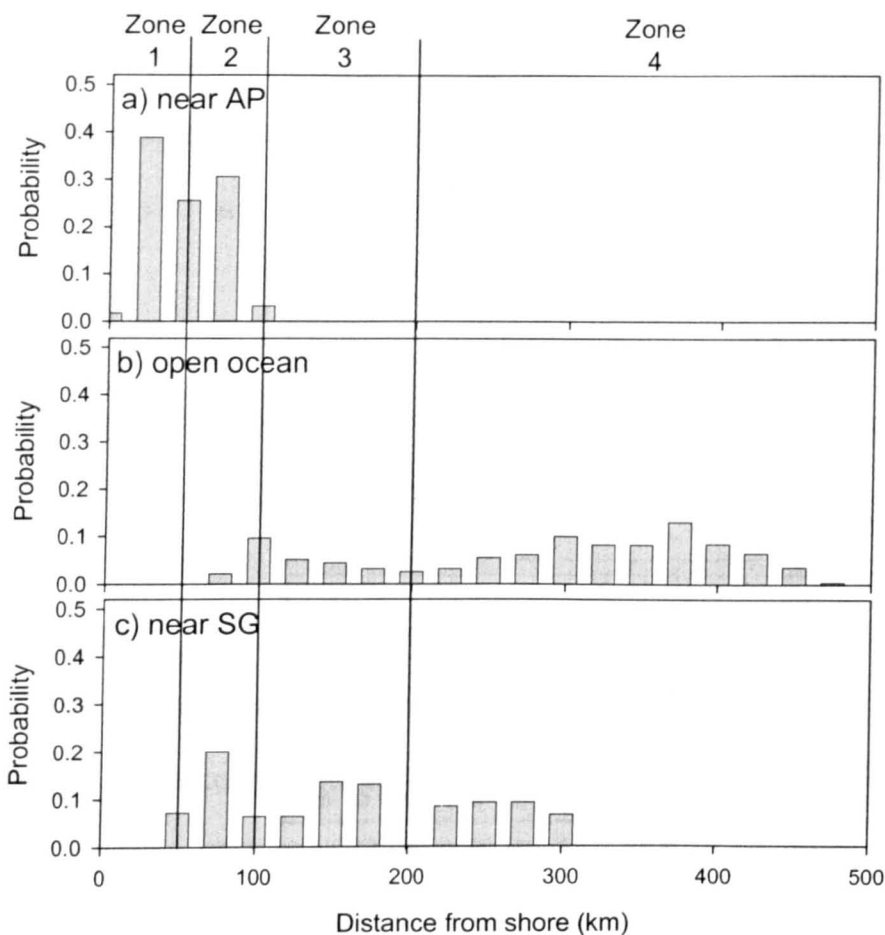


Figure 4.6. How the regions differ in terms of distance from shore. Lines indicate the boundary distances for each of the model zones.

Best estimate predictions

The first two figures in this section show the tracks of krill across the Scotia Sea, using ArcGIS maps, divided into regions that differ in terms of chlorophyll concentration and distance from land-based predator colonies. When the model was run with average chlorophyll *a* conditions, small krill displayed the same type of behaviour in each of the model-defined regions of the Scotia Sea (Figure 4.7). Their behaviour was not affected by distance to shore or changes in the concentration of chlorophyll in this simulation.

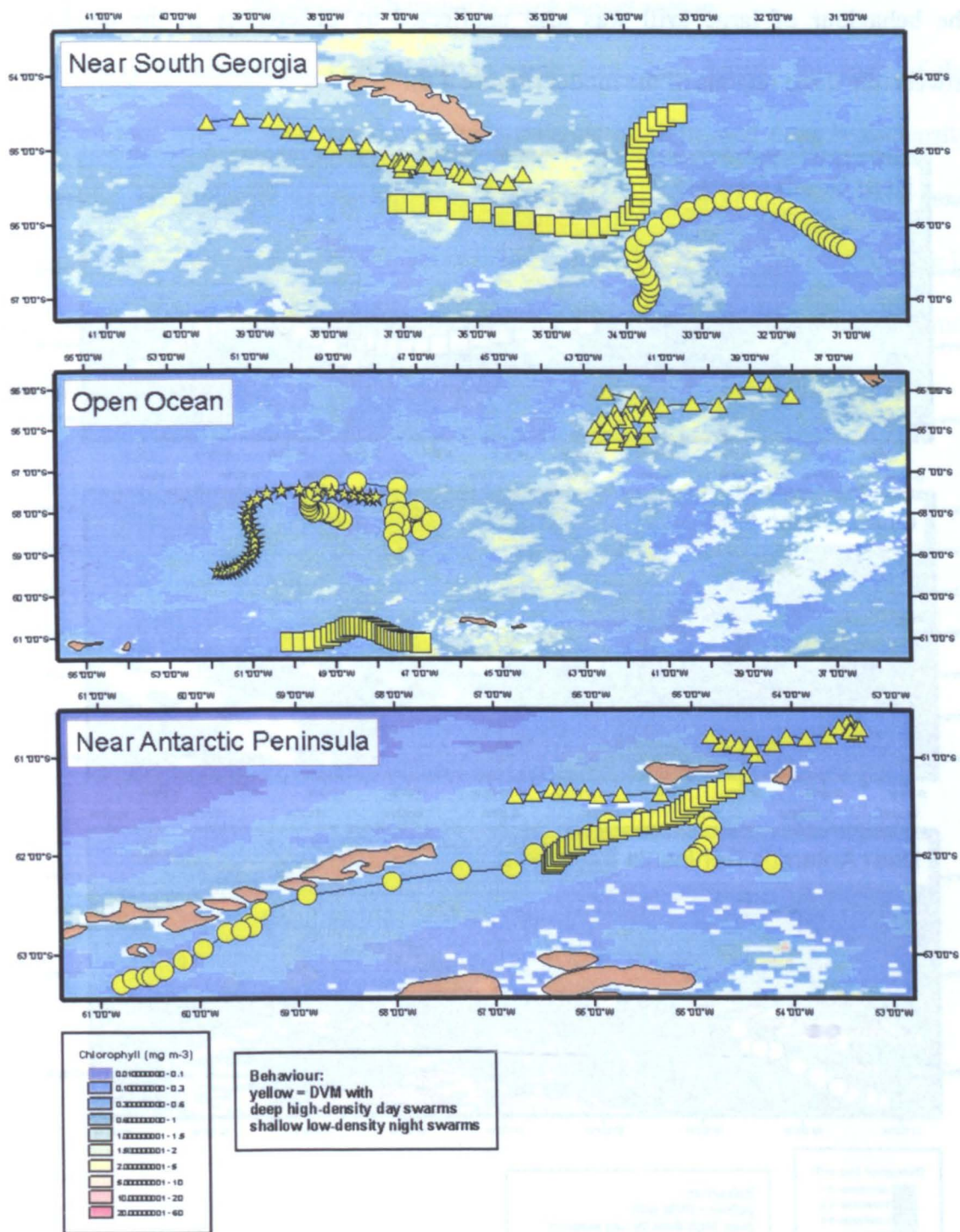


Figure 4.7. Map of the behaviour of small krill across the Scotia Sea, each track covering a period of 30 days. Krill behaviour is shown for day and night, underlayed with the mean of all global chlorophyll *a* data acquired in January from the years 2003 to 2005 (see Figure 4.3). Different symbol shapes indicate different tracks. Colour represents the type of behaviour.

The behaviour of large krill was also unaffected by differences in the conditions between the three regions of the model (Figure 4.8).

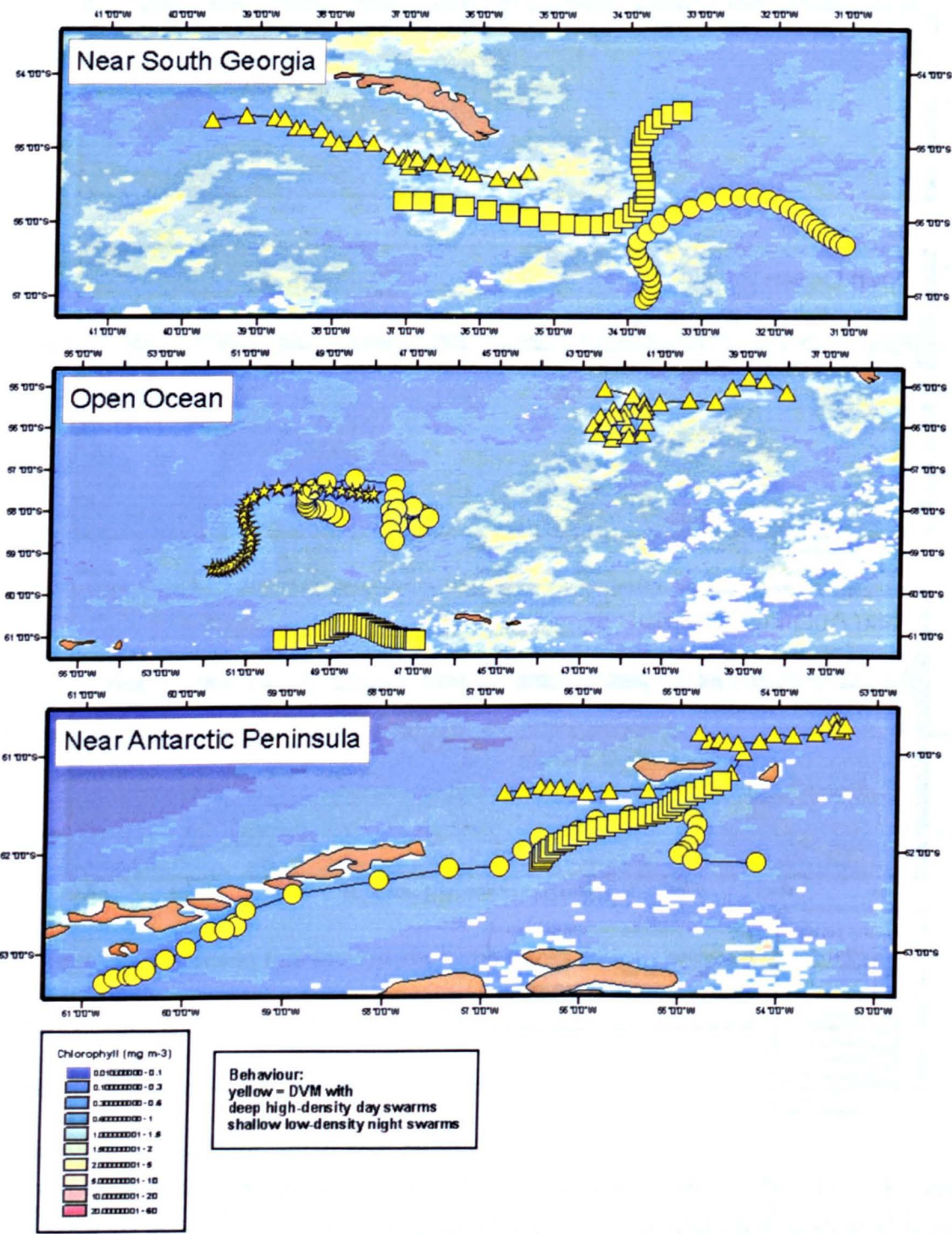


Figure 4.8. The behaviour of large krill across the Scotia Sea, each track a period of 30 days. Behaviour is shown for day and night, underlayed with mean chlorophyll *a* data for January (see Figure 4.3). Symbol shapes indicate different tracks; colour represents behaviour.

Predicted behaviour in each model region

Under nearly all conditions, krill adopt the same depth and density for each of the model regions, with shallow and low-density swarms at night, and deep high-density swarms during the day (Figure 4.9). Only small krill deviate from this behaviour, and only under high food conditions. In this scenario, small krill spend most of their time in deep low-density swarms, except in the Antarctic Peninsula region, where a small proportion of their time is spent in medium-density deep swarms during the day.

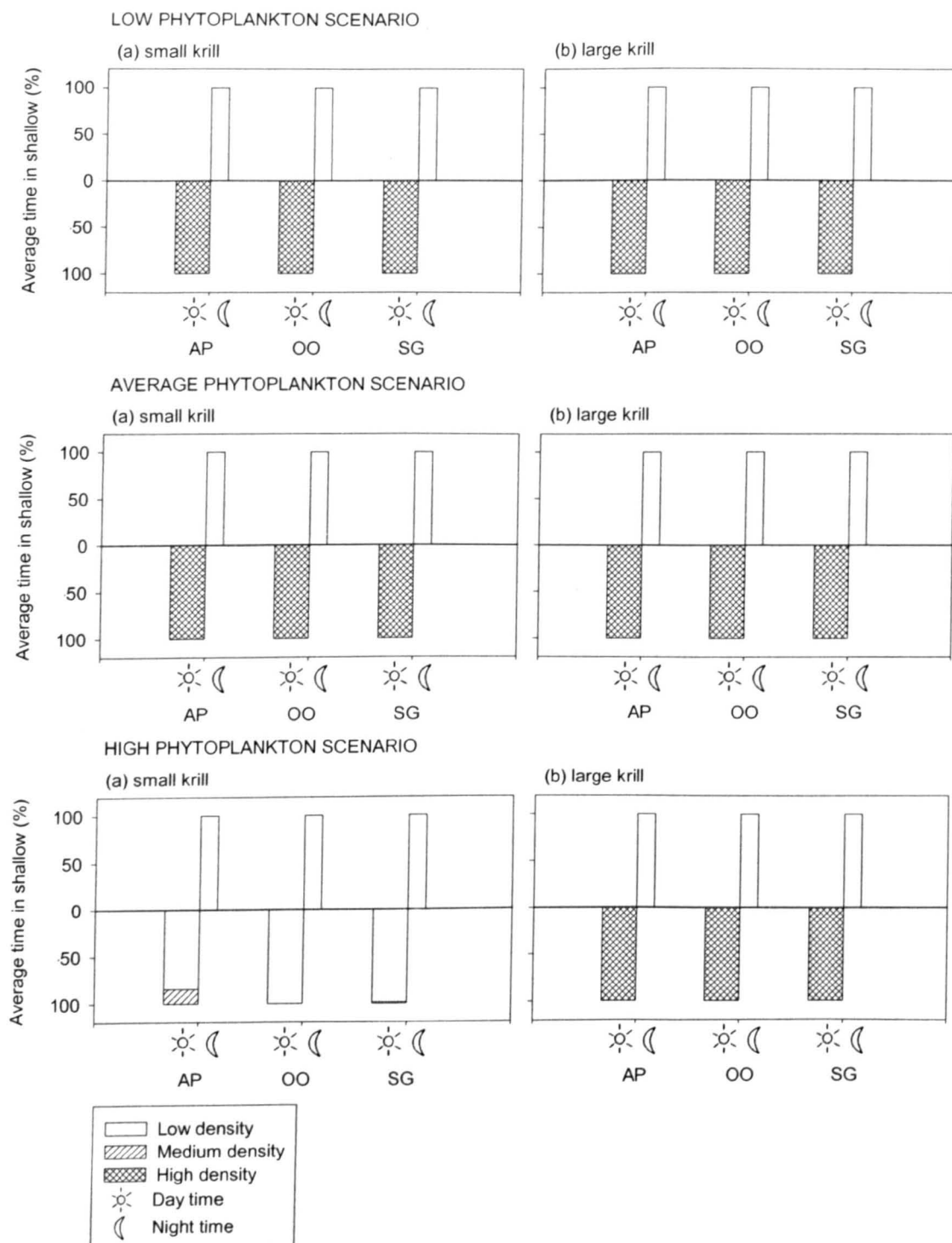


Figure 4.9. The predicted average depth and density of small and large krill during day and night in each of the zones (AP: Antarctic Peninsula, SS: Scotia Sea and SG: South Georgia), and for simulations of low, average and high phytoplankton availability.

Predicted energy levels for krill in each of the model regions

Energy level represents the amount of energy accumulated by the final time step (for the middle month) minus the amount at the initial, to give total accumulated energy for the model month of interest. The following graph shows the accumulated energy for both small and large krill in each of the regions of the model (Figure 4.10). Small krill accumulate more energy than large krill, and have a negative energy balance (representing shrinking) for low food conditions at the Antarctic Peninsula and low to average food conditions in the open ocean. Large krill have a positive energy balance in South Georgia region and open ocean regions with high food availability, and also at South Georgia with average food conditions. Overall, krill accumulate the most energy in the South Georgia region, and the least energy near the AP.

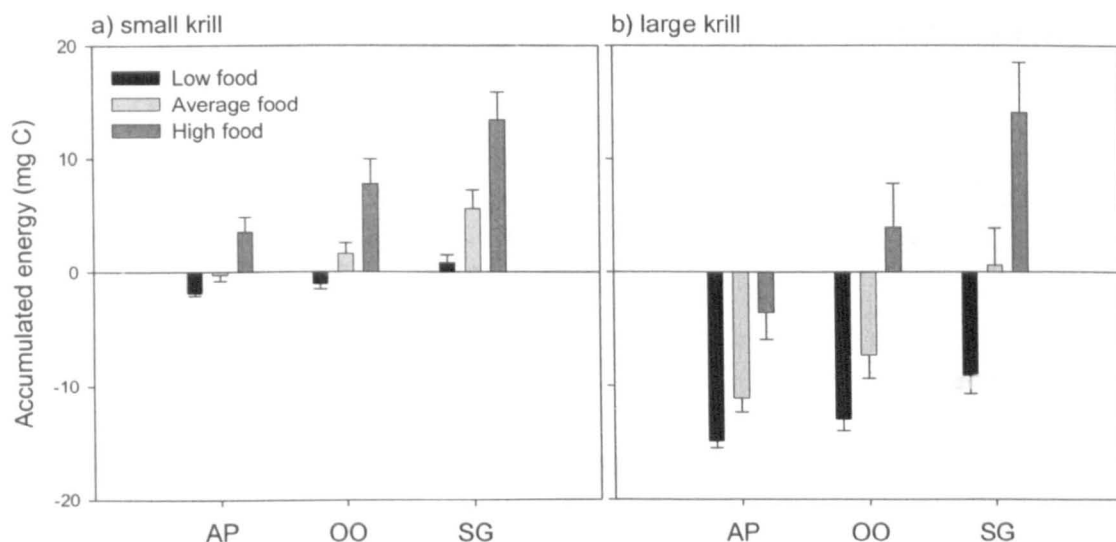


Figure 4.10. Accumulated energy for small and large krill in each of the regions (AP: Antarctic Peninsula, SS: Scotia Sea and SG: South Georgia).

Track examples

One track example was taken from each region, showing the conditions and resulting krill behaviour and energy for each. The first of these graphs shows the behaviour of small and large krill in the Antarctic Peninsula region, for (a) low and (b) high food

simulations (Figure 4.11). Here, (i) chlorophyll and (ii) distance to shore are both very low, with chlorophyll under 1 mg m^{-3} even in high food conditions, and distance less than 100 km to nearest land. All krill exhibit a classic DVM pattern, with shallow low-density swarms at night and deep high-density swarms during the day, except for small krill with high food conditions (b-iii). Here, small krill adopt deep low-density swarms at night. Small krill maintain their energy levels around the initial value, while large krill end up with a negative energy budget (v).

Antarctic Peninsula region

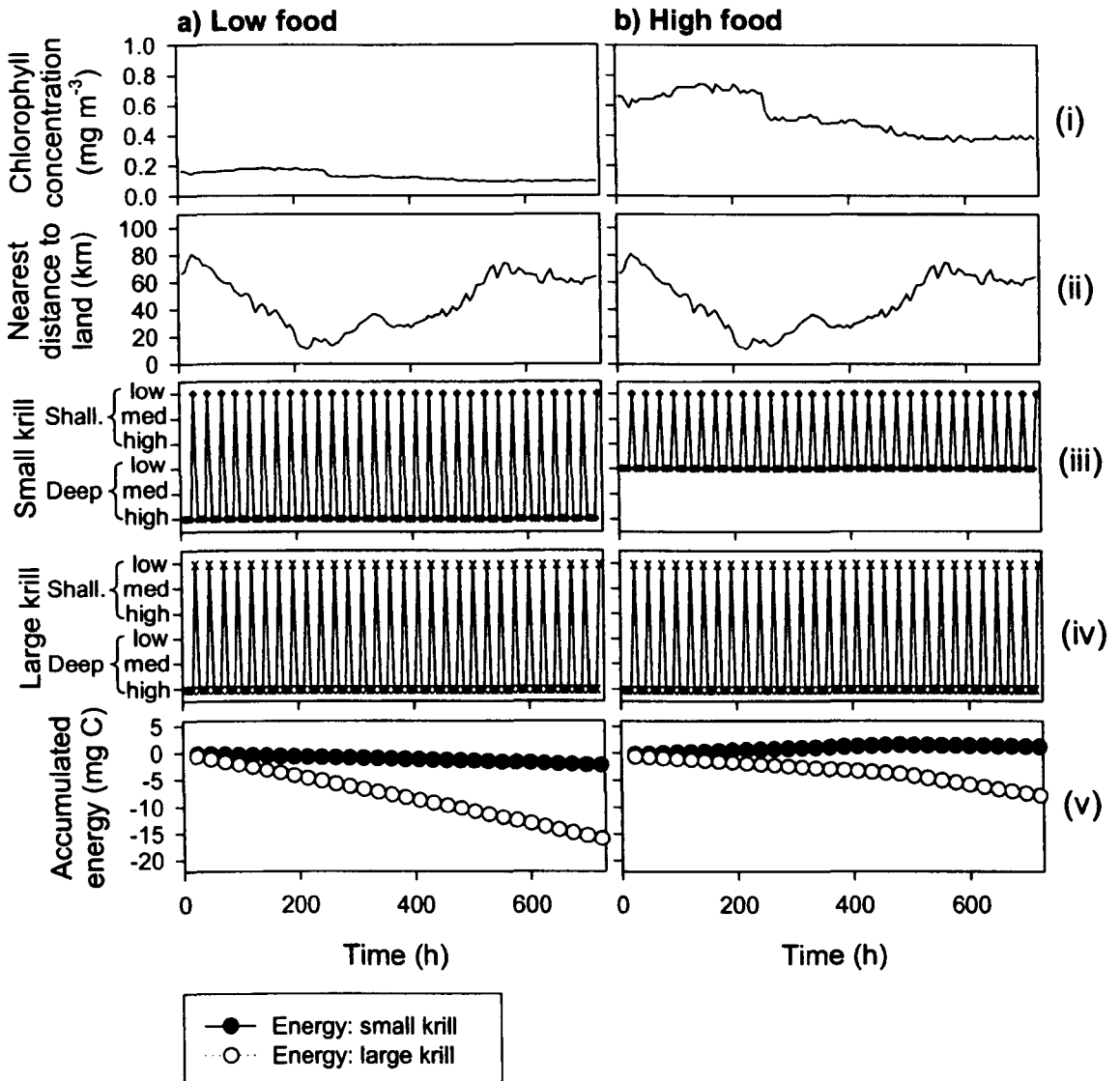


Figure 4.11. Example of the effects of changing conditions over time on the swarming and DVM behaviour for (iii) small krill and (iv) large krill and (v) energy levels for track 1 near the Antarctic Peninsula. The principle forcing functions are (i) chlorophyll and (ii) distance from shore. For (iii) and (iv) low, med and high indicates the density of swarm adopted at the specified depth.

In the open ocean region, both chlorophyll (i) and distance from shore (ii) are higher than near the Antarctic Peninsula (Figure 4.12). However, the behaviour of small and large krill in this region is the same as in the Antarctic Peninsula region, with DVM of shallow low-density swarms at night and deep high-density swarm during the day in

most conditions (iii & iv), only changing for small krill with high food conditions where swarms during the day are low-density (b-iii). Their behaviour does not change over the course of the track where distance to shore remains within the range of 200 to 500 km throughout. The model predicts DVM with low-density swarms day and night. Overall, small and large accumulate slightly more energy than in the Antarctic Peninsula region, but large krill still end up with a negative energy budget (v).

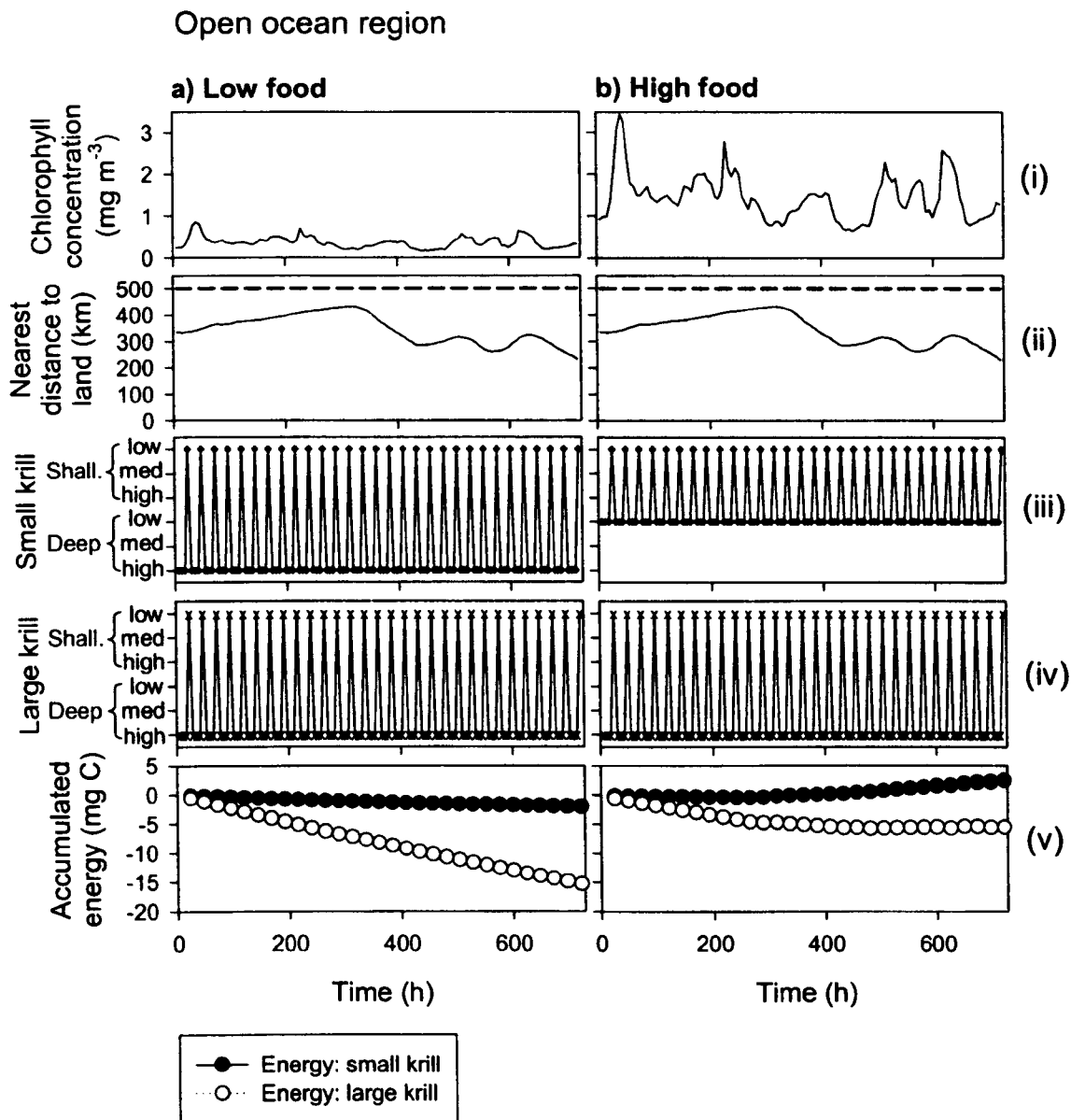


Figure 4.12. Example of the effects of changing conditions over time on the swarming and DVM behaviour for (iii) small krill and (iv) large krill and (v) energy levels for track 5 in the open ocean region. The principle forcing functions are (i) chlorophyll and (ii) distance from shore. For (iii) and (iv) low, med and high indicates the density of swarm adopted at the specified depth.

At South Georgia, the situation is different (Figure 4.13). Chlorophyll concentration is much higher than in other two regions (i), and this has a positive effect on the energy accumulated by krill, particularly in high food conditions (b-v). This scenario is the only out of the chosen tracks where large krill have a positive energy balance over time

(b-v). The behaviour of krill is DVM with deep high-density day swarms and shallow low-density night swarms most of the time (iii & iv). The exception again occurs for small krill in high food conditions (b-iii), that adopt low-density DVM except when distance from shore drops to zone 1 (< 50 km) and they switch from deep low-density to deep high-density day swarms. The scenario at South Georgia with high food concentration is also the only example, out of the selected tracks, where large krill end up with a greater accumulated energy than small krill (v).

South Georgia region

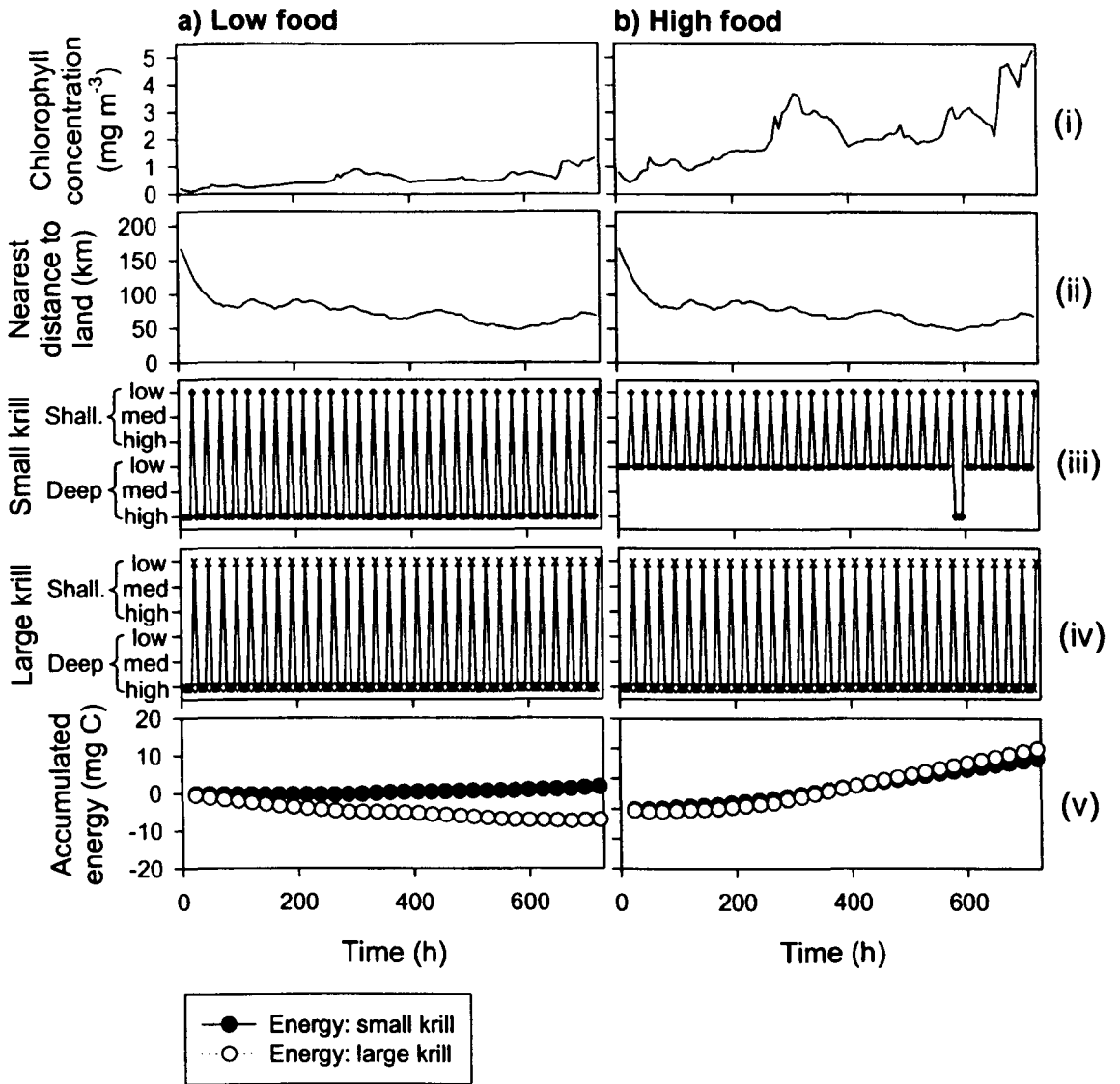


Figure 4.13. Example of the effects of changing conditions over time on the swarming and DVM behaviour for (iii) small krill and (iv) large krill and (v) energy levels for track 5 in the open ocean region. The principle forcing functions are (i) chlorophyll and (ii) distance from shore. For (iii) and (iv) low, med and high indicates the density of swarm adopted at the specified depth.

Sensitivity analysis

The sensitivity of the model was calculated by dividing the % change in the result by the % change in the variable tested. If the result was already in the form of a proportion

or percentage then absolute change in the result was divided by the percentage change in the variable.

$$Flex = \frac{\Delta result}{\Delta parameter} \%$$

The energy result was most sensitive to changes in the parameterisation of food availability and background carbon level, with the energy level of large krill being more sensitive to changes in the parameter values than small krill (Figure 4.14). The energy accumulated by krill was only slightly affected by changes in the terminal reward and maximum clearance rate.

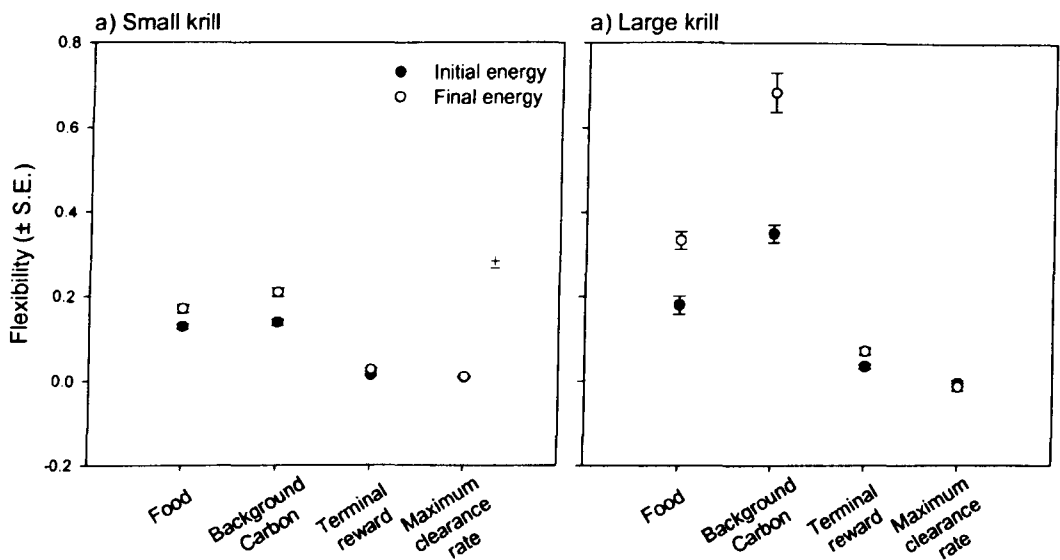


Figure 4.14. Flexibility of energy result for each of the parameters specifying food level, background carbon, terminal reward and maximum clearance rate.

Krill depth was most affected by changes in the background level of heterotrophic carbon, although the depth of krill at night was not affected by changes to any of the

parameters (Figure 4.15). The second most sensitive parameter affecting krill depth was food availability.

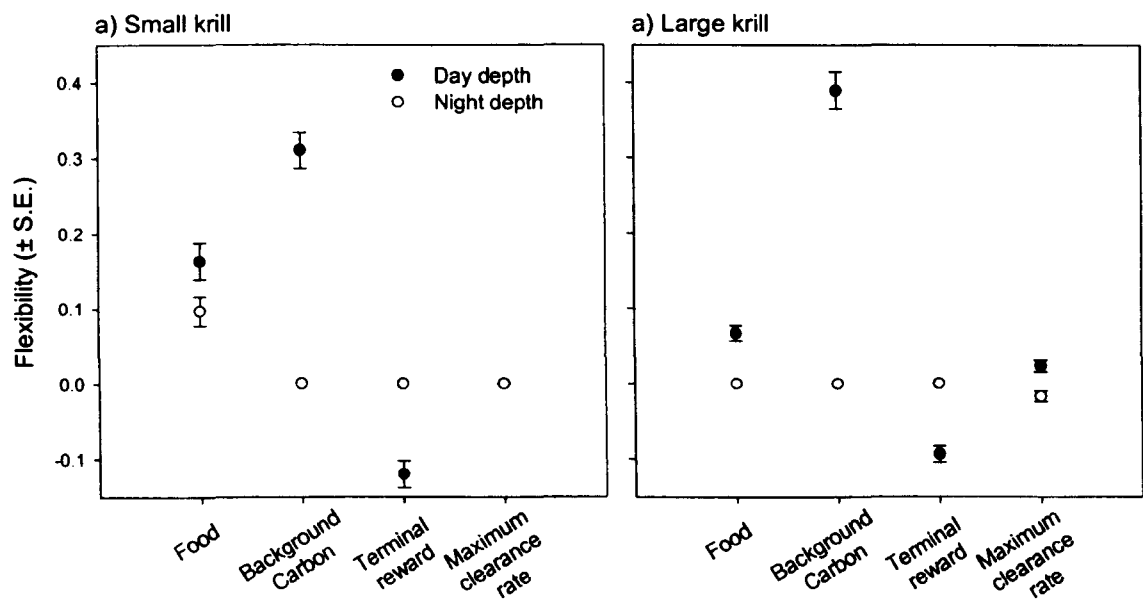


Figure 4.15. Flexibility of each of the parameters to the krill depth result.

The density of swarms during the day, for small and large krill, was equally affected by changes in parameter values (Figure 4.16). Again, the result was most strongly affected by the background level of heterotrophic carbon and secondly by changes in food availability. The density of swarms was not affected noticeably by the terminal reward or maximum clearance rate.

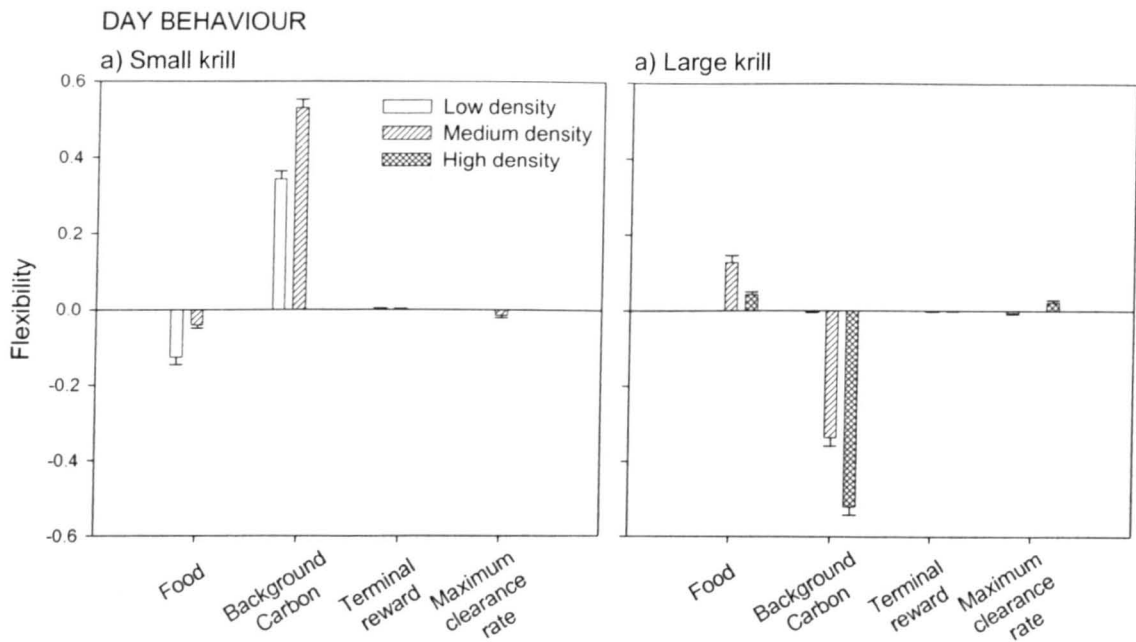


Figure 4.16. Flexibility of the krill swarming behaviour during the day, for low, medium and high density swarms.

Swarm density at night was not sensitive to changes in parameter values (Figure 4.17).

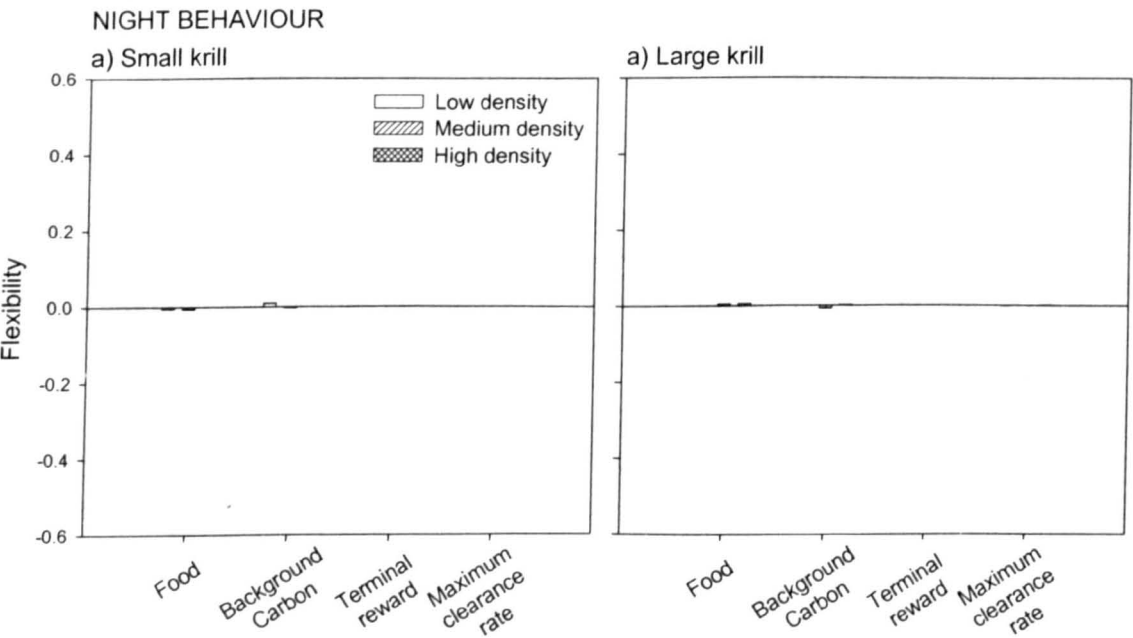


Figure 4.17. Flexibility of the krill swarming behaviour at night, for low, medium and high density swarms.

DISCUSSION

DVM in the Scotia Sea

The predicted DVM pattern of krill in all regions of the model was relatively uniform. From the Antarctic Peninsula across the Scotia Sea to South Georgia, all krill were predicted to adopt depths in the upper part of the water column at night and deep water during the day over low, average and high food conditions. Predicted DVM remained the same when krill were both within reach of predator colonies where mortality was higher, and in open ocean regions where mortality was lower. This is probably because the benefit of feeding in the shallow water during the day never outweighed the risk of mortality in any region. In other words, the estimates of relative mortality between day and night would have to be very different to change the predicted pattern of DVM.

DVM was first reported over 180 years ago (Cuvier 1817) and is believed to be the result of a trade-off between minimising predation risk and maximising food intake (Burrows and Tarling, 2004; De Robertis, 2002; Eiane and Parisi, 2001; Gilliam and Fraser, 1987; Godlewska, 1996; Hays, 2003; Russell, 1927). The amplitude and timing of DVM does not follow a simple pattern and can depend on a number of environmental factors (Everson, 1983; Godlewska, 1996). As a result, there are a wide variety of vertical migration patterns associated with krill (Godlewska, 1996; Loeb and Shulenberger, 1987) including midnight sinking (Tarling et al., 2000) and reverse migration, which has been observed in the region of South Georgia (Godlewska, 1996; Kalinowski, 1978). Some authors suggest that variety in DVM is evidence of behavioural flexibility rather than strict genetic programming (Hays, 2003; Verity and Smetacek, 1996). Indeed, there is some evidence that the range of DVM can change given different environmental conditions (Tarling et al., 2000). However, it is unknown

at what scale krill can respond to changes in environmental conditions, with some suggesting weeks or less (Ross et al., 2000). The environmental conditions across the Scotia Sea in January are highly variable in terms of chlorophyll, mortality and currents (Korb et al., 2004; Reid et al., 2002; Thorpe et al., 2004). However, the results from this model suggest that, even when faced with these highly variable conditions, krill may not alter their DVM pattern but adopt a stable DVM throughout this section of the journey. This strategy is consistent over years of high and low chlorophyll availability and is robust over changes in other parameter variables.

Swarm density across the Scotia Sea

Diel patterns in swarm density under average chlorophyll conditions

The predicted density of krill swarms across the Scotia Sea did not change with proximity to predator colonies or local chlorophyll patchiness under average food conditions, showing a consistent diel pattern. Krill swarms were shallow and low density at night, deep and high density during the day. The diel pattern allowed krill to maximise food intake by feeding in low-density swarms at night, and to minimise predation while also saving energy by adopting deep high-density swarms during the day. The swarm density adopted by krill during the day was most sensitive to changes in food availability and the parameterisation of background heterotrophic carbon, highlighting the importance of obtaining quantitative estimates of alternate food sources for krill. Swarm density at night was insensitive to nearly all changes in parameter values.

Swarm density of krill represents a trade-off, like DVM, between minimising predation risk and maximising food intake, where one is achieved at the cost of the other. As with

DVM, this trade-off will vary through a diel cycle as changing light levels alter predator capture ability and prey vulnerability (Mangel and Clark, 1988). Proposed benefits of swarming include reduced predation, through group avoidance strategies and increased vigilance (Obrien, 1987; Ritz, 2000), and reduced respiration, from hydrodynamic advantages of swimming alongside neighbours (Ritz, 2000; Ritz et al., 2003). The major cost of dense swarming is reduced ingestion due to intraspecific competition for food (Morris et al., 1983; Ritz, 2000). There is circumstantial evidence from acoustic studies for a diel rhythm in swarming, where krill disperse in shallow swarms at night for feeding then reform into deep high-density swarm during the day (Croxall et al., 1985; Everson, 1982; Godlewska, 1996; Witek et al., 1981). However, there is little experimental evidence for this, as schooling behaviour is inherently difficult to study in both the field and the laboratory (Hamner and Hamner, 2000; Hofmann et al., 2004; Strand and Hamner, 1990; Swadling, 2005). As a result, there is little understanding of the stability of the observed diel pattern in swarming under different levels of mortality and food abundance. Both aspects are likely to be highly variable across a heterogeneous region such as the Scotia Sea. Thus far, the model predicts a stable strategy of swarming behaviour, low density swarms at night and high density swarms during the day, throughout the Scotia Sea during January under a range of food conditions.

Although there is very little direct evidence for krill swarming behaviour in the laboratory or the field, there is a better understanding of schooling in fish, which are larger and easier to study. In fish shoals, work reveals that individuals constantly reappraise the costs and benefits of being social (Pitcher, 1986). Variation in the intensity of schooling behaviour in fish suggests that the benefits of aggregation are

balanced by certain costs (Sogard and Olla, 1997). The aggregation of pelagic fish into schools or shoals is presumed to confer potential benefits of reduced predation risk, achieved through a variety of different mechanisms (Pitcher and Parrish, 1993). Different to our assumptions in this chapter is that schooling for fish results in increased foraging success (Sogard and Olla, 1997). For example, Milne *et al* (2005) reported lake herring, *Coregonus artedii*, stomach fullness increased with school size, suggesting that schooling enhances foraging opportunities for individual members. Other studies have suggested this may be the case for krill as well (Hofmann et al., 2004), although there is no direct evidence. There is some evidence for size differences in schooling fish, with small juveniles maintained on high rations being highly responsive to the potential threat of a predator, with groups becoming more cohesive and remaining so for up to an hour after the initial threat (Milne et al., 2005). Large juveniles, however, did not change their degree of aggregation in response to predation threat (Milne et al., 2005). It is useful to compare the schooling behaviour of krill to that of fish, although it is unwise to assume too much. Aggregation can be regarded as part of a continuum in group integration: at one end, territorial animals with little need to engage in information transfer and no need for group structure; at the other, highly integrated, long-term associations between individuals of a group, with potentially high rates of direct and indirect information exchange (Parrish et al., 2002). We still have little idea of where Antarctic krill come on this continuum, but suggest a lot more research is required.

Size-dependent differences in swarm density

The only exception to the observed pattern in swarm density described above occurred for small krill under high chlorophyll conditions. In this scenario, small krill could be

found in low-density, instead of high-density, deep swarms during the day, except when they were very close to land. Less than 50 km from land, small krill adopted a higher density swarm during the day. It is likely that low-density deep swarms were predicted under high food conditions only for small krill because the increased food intake outweighed the increased respiration from dispersing. Large krill have a higher respiration than small krill, so the increased respiration cost of low-density dispersed swarms in the deep water outweighed the benefit from increased food intake. When small krill were less than 50 km from land, the increased risk from predation tipped the balance of the trade-off, such that the increased food intake from dispersing no longer outweighed the increased risk of predation, even though krill were deep in this high-mortality zone. These results suggest that the conditions in the Scotia Sea are such that krill should only respond to increased predation when food concentration is high and respiration costs are low, i.e. for small krill only.

The swarm density predictions for small krill were most sensitive to changes in the availability of food and the parameterisation of heterotrophic background carbon. Swarm density of large krill was not sensitive to these changes in food availability. It is important to interpret these results then only qualitatively, because the parameterisation of heterotrophic carbon is inherently difficult. This, however, also highlights the importance of obtaining accurate estimates for this parameter, particularly if assessing differences in the behaviour of small and large krill across the Scotia Sea.

Potentially different swarm densities for small and large krill in the field can arise from differences in the trade-off between minimising predation and maximising food intake. Although this trade-off is one of the most commonly observed in biology, its

investigation in invertebrates, particularly in social aquatic species, is uncommon (Ritz, 1994). The main difference in the size specific trade-off is due to small krill having both a lower rate of filtration and cost of respiration than large krill (Hofmann and Lascara, 2000). In addition, size-specific predation on krill may account for differences in the trade-off (De Robertis, 2002; Hill et al., 1996; Reid et al., 1996), although apparent evidence of size selection by predators may be due to differences in the distribution of krill size classes. There is field evidence, from acoustic and net sampling, of small krill choosing riskier habitats than large krill, both in terms of depth (Loeb et al., 1993) and density (Daly and Macaulay, 1991), with observations of deeper and denser swarms of large krill and shallow, more dispersed swarms of small krill near Elephant Island and the South Shetland (Brinton et al., 1987). Further experimental or observational evidence is however lacking. While there has been some work into swarm classification in terms of shape and composition (Ricketts et al., 1992), much less is known about the biological characteristics of krill within swarms and biological variance between swarms (Burrows and Tarling, 2004). I predict a more dispersed, risky, swarm density habitat for small krill compared to large krill in years of high phytoplankton abundance, due solely to differences in the trade-off between mortality and food brought about by small krill having lower respiration and filtration rates than large krill, as there was no size-specific mortality in the model.

Energy

Size dependent energy accumulation

Small krill accumulated more energy in the model in absolute values, mg C, than large krill in all scenarios except under the highest food conditions at South Georgia, where large krill accumulated the same amount of energy as small krill. The difference was

most sensitive to changes in the overall availability of phytoplankton, followed by the parameterisation of the heterotrophic component of the diet. The accumulated energy of large krill was much more sensitive to changes in these parameters than the result in energy balance of small krill.

Overall, food concentration is believed to have the greatest effect on krill growth (Atkinson et al., In press, Ross, et al., 2000), which is consistent with the model results of this chapter. However, there is evidence in the field of differing growth rates for small and large krill, where growth rate decreases with increasing krill length independent of food concentration (Atkinson et al., In Press; Ross et al., 2000; Siegel et al., 2004; Tarling et al., 2006). Different growth rates in the field may arise from differences in temperature (Atkinson et al., In Press; Fach et al., 2002; Quetin et al., 1994), food quantity and quality (Ross et al., 2000; Ward et al., 2005), or differences in energy allocation, with large krill allocating more energy to reproduction than small krill (Atkinson et al., In Press). In addition, the interaction between these factors is complex, with some authors reporting growth increasing with increasing temperature (Fach et al., 2002; Hofmann and Lascara, 2000) and others the opposite (Atkinson et al., In Press). The current model predicted that small and large krill should grow at different rates. However, factors such as temperature, allocation of energy to reproduction, and quality of food were not considered. I predict that small krill should accumulate more energy than large krill when food availability is as variable as that found in the Scotia Sea, predominantly due to a lower cost of respiration for small krill.

Krill shrinkage

The energy budget of large krill (i.e. assimilated energy minus respiration) was negative under most conditions across the Scotia Sea. This is possibly due to the high cost of respiration for large krill and also the fact that, to maximise fitness, krill were minimising mortality by adopting DVM and high density swarms at the cost of food intake. However, one must also take into account the importance of correctly parameterising the contribution of heterotrophic food to the diet, as indicated by the sensitivity analysis. It is possible that heterotrophic food levels will be greater than those used in the model in the regions where chlorophyll was sparse.

A unique aspect of krill growth and ecology is that krill can shrink under unfavourable conditions such as low chlorophyll, high temperature, or possibly in response to high predation (Alonzo and Mangel, 2001; Hofmann and Lascara, 2000; Ikeda and Dixon, 1982; Nicol, 2000; Quetin et al., 1994). However most predict krill shrinkage over winter not summer conditions. For the low chlorophyll conditions of the Scotia Sea there are conflicting data. Models on krill energetics predict krill shrinkage across the Scotia Sea in low chlorophyll areas, particularly for large krill which may therefore require additional food sources such as copepods, dinoflagellates and ciliates (Fach et al., 2002; Hofmann and Lascara, 2000). However, Atkinson *et al.* (In Press) found that, even in the low chlorophyll zones of the central Scotia Sea, all swarms maintained a mean positive growth. A length frequency analysis in the same study revealed a much lower proportion of large krill in the low chlorophyll Antarctic Peninsula region of the Scotia Sea and a higher proportion of large krill in the higher chlorophyll, South Georgia region, which could account for differences in the growth rates of the above authors. If large krill were present in the south of the Scotia Sea, a mean negative

growth rates may have been observed. However, even in the typically low chlorophyll central Scotia Sea, both small and large krill had positive growth rates (Atkinson et al., In Press). Differences in the prediction of negative energy budgets could also stem from an inadequate understanding of krill omnivory. Evidence for krill eating a range of food other than phytoplankton is clear (Atkinson and Snyder, 1997; Price et al., 1988; Ross et al., 2000). However, there is little understanding of the exact contribution of heterotrophic food and detritus to the carbon budget of krill and how this contribution changes with factors such as temperature, depth and chlorophyll concentration. I predict shrinkage for large krill under nearly all conditions of the Scotia Sea. Further quantitative research into both the respiration of krill of varying sizes and the heterotrophic component of the diet is needed before this inconsistency can be understood. In addition, the effect of mortality on growth is not well understood. The fact that large krill did not alter their DVM or swarming pattern despite having a negative energy budget demonstrates the strong influence that mortality can have on growth.

The journey

In nearly all conditions on the journey across the Scotia Sea, krill did not change their behavioural strategy in response to highly variable conditions. The exception was for small krill in high food conditions that adopted more dispersed swarms, in certain circumstances. The lack of a predicted behavioural response to the level of environmental variability observed in the Scotia Sea suggests an overestimate of the difference in mortality between day and night or shallow and deep habitats such that a change of DVM or swarming strategy would result in too great a cost to fitness.

In terms of their life history, krill may be able to cope with variability because of their long lifespan (Brinton et al., 1987), the fact that they can shrink under a negative energy budget (Quetin et al., 1994), and their behavioural plasticity in terms of the formation of swarms and DVM. There is circumstantial evidence that krill may respond to their environment in weeks or less, the same timescale as changes in phytoplankton may occur (Ross et al., 2000). However, when transported at a relatively fast speed across constantly changing conditions, I predict a stable strategy of DVM and swarm density, even when this results in a negative energy budget. I also predict that krill only respond to local changes in mortality and food when both are at their highest, which is perhaps why the occurrence of anomalous behaviour such as reverse migration and day swarming have been observed at South Georgia where mortality and food are at their highest, and less so in other areas.

SUMMARY OF FINDINGS

- The DVM strategy of small and large krill was constant across all regions of the Scotia Sea under years of low to high chlorophyll abundance and in response to locally variable chlorophyll and predation risk.
- There was a stable diel pattern in swarm density for small and large krill, which did not change under average chlorophyll concentrations, but differed for small and large krill in high chlorophyll years.
- Small krill only responded to proximity of predator colonies when both food concentration and mortality were at their highest.
- Small krill accumulated more energy than large krill, in absolute terms, under all conditions and regions of the Scotia Sea, due to a lower respiration rate.

- Shrinkage was predicted for large krill under most conditions in the Scotia Sea, highlighting the importance of obtaining accurate estimate of both respiration and heterotrophic food for krill.
- Krill are predicted to respond with a stable strategy to highly variable conditions over the time scale of one month, for their journey across the Scotia Sea to South Georgia.

FUTURE VALIDATION

I recommend the following experiments to test the predictions made in this model.

- Acoustic measurements of DVM across the Scotia Sea during January to determine whether krill have a stable pattern of behaviour in different regions and over years of high to low phytoplankton availability.
- Using nets and acoustics to examine diel patterns in krill swarm density, and further to determine the stability of the diel pattern in different regions of the Scotia Sea over years of different food concentration.
- Using nets and acoustics to examine differences in the swarm densities of small and large krill in years of high phytoplankton abundance, to determine if small krill are in more dispersed swarms in these years.
- Further work into the heterotrophic component of the diet for *Euphausia superba*.

5.

THESIS DISCUSSION

MAIN FINDINGS

In this thesis, I have successfully applied three distinct but theoretically linked models to investigate the behaviour of two key species in the Southern Ocean, macaroni penguins and Antarctic krill. The main findings of the study consist of predictions relating to how macaroni penguins may respond to a changing krill resource (availability and variability) during the breeding season, and how krill in turn respond to changing predation and food conditions in different areas of the Scotia Sea.

The first major prediction is that macaroni penguins will incur the cost of travelling further from the nest in order to obtain a more reliable meal of krill, even if the reward of krill does not change with distance from nest. This result suggests that it is not just the krill availability but also the variability of the krill resource that affects foraging behaviour of macaroni penguins during the breeding season. The second important finding of the thesis relates to behavioural mechanisms that may be employed by krill to influence their distribution. Around South Georgia, I demonstrated that krill are able to increase their overall concentration in favourable areas without sensing gradients in the environment or being advected by currents, but simply by altering their swimming speed and turn rate depending on conditions for feeding and mortality. This behaviour led to a higher predicted concentration of krill at the shelf-break, a region where krill are known to be particularly abundant (Trathan et al., 2003). The third major finding of this

thesis describes the likely existence of a threshold availability of krill to penguins, below which the female penguin does not return to the nest and the chick most likely dies, and above which the female keeps a constant supply of food to the chick at the cost of her own body condition.

DIRECTIONS FOR FUTURE RESEARCH

The recommendations are as follows:

- Combine krill acoustics and net sampling around South Georgia with chick growth and female mass during the guard stage to determine if there may be a threshold level of krill density close to South Georgia, below which chicks fail, and above which chicks fledge at around a normal weight.
- Use nets and acoustics to compare the depth and density of krill swarms near islands to those in open ocean regions. This would help determine if the DVM of krill is generally constant across open ocean regions, but less predictable close to an island, and also if there is a detectable diel pattern in the density of krill swarms in open ocean regions.
- I recommend further research into the heterotrophic component of the diet of Antarctic krill. This is based on the sensitivity of the krill model (Chapter 4) to changes in the heterotrophic carbon content of the diet. In addition, I recommend further work into the swarming behaviour of krill; both behavioural work in the field and further attempts to quantify the effect of swarming/schooling on krill respiration, filtration and mortality.

DISCUSSION

An evaluation of the modelling technique used in the thesis

The State Dynamic Programming (SDP) modelling technique was useful in answering the questions posed in this thesis, producing simple predictions that were robust across a range of parameter values. An attraction of SDP models is that experiments chosen because of their tractability in the field can be mirrored by experimental manipulations on the computer, either by a change of state or by a change in parameter values (Houston & McNamara, 1989; Hutchinson & McNamara, 2000). In addition, the approach allows for a number of behaviours to be considered both simultaneously and sequentially, with physiological and environmental constraints easily incorporated into the framework (Mangel & Clark, 1988). In testing the sensitivity of the model to the parameter values it was also possible to reveal whether the model was insensitive to variation in some parameters, in which case measuring their values would be unnecessary. It was also possible to determine whether more information about other parameters would be required in order for the model to make accurate predictions, so giving a stimulus for further field campaigns (Hutchinson & McNamara, 2000).

The SDP technique worked particularly well in this thesis for modelling the behavioural decisions of female penguins feeding their chick (Chapter 2). Fitness in this case was considered in terms of the body condition of the parent and growth of the chick (future and current reproductive success). One of the difficulties in this model was quantifying mortality risk. I assumed no risk of mortality for the female penguin during the guard stage based on the assumption that there was little risk of death at this time to macaroni penguins. Risk of death, other than starvation, arises because of predation by leopard seals (Jansen et al., 1998). These predators are based around Antarctic and sub-

Antarctic islands mainly during winter and early spring (Jessopp et al., 2004; Rounsevell & Pemberton, 1994). In summer, during the penguin breeding season, numbers are lower, but there is much variation in their numbers at sub-Antarctic locations from year to year (Borsa, 1990; Walker et al., 1998), meaning there could be a possible impact on penguin foraging behaviour during chick rearing. This may be an important factor to test in future models of the situation at South Georgia.

In the models on krill behavioural decisions in this thesis, mortality was difficult to parameterise; particularly how mortality was affected by changes in the density of swarm adopted by krill. There was very little information in the literature on which to base this parameterisation, with the only experimental study on zooplankton swarming based on mysids, not krill (Ritz, 2000; Ritz et al., 2001; Ritz & Metillo, 1998). This feature of krill behaviour has largely been ignored in both experimental work and models of krill behaviour, due to the fact that krill are hard to study in the field (Hamner & Hamner, 2000), that they do not school in the laboratory (Swadling et al., 2005) and that this behaviour adds significant complications to the study of krill population dynamics (Watkins et al., 1986). I suggest a different modelling approach would be more useful for attacking this problem.

On a small scale, the behaviour of an individual in a school or flock can be simulated by a few very simple rules: these simulations are known as boids (Reynolds, 2001). For example, the flocking of birds can be described by the three rules: that each individual stay within a certain average distance to its three closest neighbours; that each individual travel at the average speed of its three closest neighbours; and that each individual travel in the same average direction as its three closest neighbours. Models

known as cellular automata also work on this concept, where individuals interact with their neighbours based on rules determining birth, movement, feeding and death (Wolfram, 1984). Stochastic cellular automata include probabilities in the outcome of interactions and rules for recruitment and mortality, removing a large degree of pre-determination by the modeller. This factor would benefit the krill-swarms problem, where there is little experimental evidence on which to base the parameter values. The cellular automata technique may better allow for answering questions such as at what scale do krill respond to predators: do krill 'remember' encounters with predators or is it just an immediate response; how far away is a predator when krill respond to it, and can this change with increased vigilance from larger swarms?

Krill are mysterious

There is little doubt that krill are of central importance in many ecosystems, and particularly so in Antarctic food webs (Marr, 1962; Mangel & Nicol, 2000; Fraser, 1936). However, there are still considerable uncertainties about key elements of krill biology and the forces that determine its distribution and abundance (Nicol, 2003). These gaps in knowledge relate most often to aspects of the behaviour of krill, which is sometimes misunderstood due to problems in studying krill both in the laboratory and *in situ*. It is important to investigate these areas of krill behaviour because assumptions one way or another can have large consequences: for example, assuming that krill could influence their position had a large effect on their distribution in the krill model of Chapter 3. Management of ecosystems where krill are either harvested components or are critical in dietary elements for other harvested species will certainly require a more detailed knowledge of their behaviour and ecology (Nicol, 2003), particularly in addressing the areas of their behaviour we least understand.

Planktonic versus nektonic

The first conceptual problem with krill is that they are generally classified as planktonic zooplankton: “animals of rather small size, which float and drift in the water layers” (Nicol, 2003). However, other studies indicate that krill should be classified as nekton as they have a strong swimming capability and may be able to actively migrate (Hamner & Hamner, 2000; Siegel, 1988; Kils, 1981). The problem is most likely that krill can sometimes behave as planktonic organisms, for example, when currents are fast and they are advected through changing conditions too quickly to respond, while at other times they may behave as nektonic organisms, perhaps where currents are slow and they are able to influence their position by adjusting their swimming behaviour. Certainly it is understood that earlier life stages of krill can be classified as planktonic with a fair amount of confidence.

In the thesis, I tested one model where krill were mainly planktonic (Chapter 4) and one where they were predominantly nektonic (Chapter 3) with regard to their horizontal position. The results suggested that, when krill behaved as nektonic organisms and currents were slow, they were able to maintain their position in favourable areas, or disperse from unfavourable areas, simply by a modification of their swimming speed and turn rate. This finding, however, is dependent on the assumption that krill have evolved the capability of recognising a favourable area compared to an unfavourable area, which may be an unreasonable assumption. Other studies on the subject suggest that krill may be able to sense gradients, moving to areas of greater food through passive information transfer through the swarm (as demonstrated in fish) (Hofmann et al., 2004; Pitcher, 1986). Hofmann et al. (2004) have tested this through the use of a

lagrangian modelling technique, which provided some crucial insights into the problem, but I believe this could also benefit from the use of other techniques.

Swarming versus schooling

Another mystery regarding the classification of krill is in terms of their level of aggregation. Aggregation itself can be regarded as part of a continuum in group integration: at one end are territorial animals with a reduced need to engage in information transfer and little need for group structure; at the other, highly integrated individuals of a group, with long-term associations and potentially high rates of direct and indirect information exchange (Parrish et al., 2002). Unfortunately, we still have little idea of where Antarctic krill come on this continuum, i.e. whether they are swarming or schooling organisms. The difference between the two is that swarming, like shoaling in fish, refers to individuals that group together for social reasons, with no implications for structure or function (Hamner & Hamner, 2000; Pitcher, 1986). Schooling, on the other hand, implies that individuals are synchronised, polarised and structurally spaced (Hamner & Hamner, 2000; Pitcher, 1986). In the model, it was assumed that krill were schooling animals, with a number of costs and benefits relating to the density of school adopted. In general, it was assumed that predation risk, food intake and energy usage decreased with increasing density of school. However, these benefits and costs were difficult to parameterise due to a definite lack of data on krill schooling behaviour. Here, it is useful to draw comparisons with the schooling behaviour of fish, which has been better studied.

One of the main assumptions in the krill behavioural models of this thesis was that krill gain an energetic advantage from higher density schooling, due to hydrodynamic effects

from neighbours. This assumption was based on experimental studies on mysids, where oxygen consumption decreased with increasing school density (Ritz, 2000; Ritz et al., 2001; Ritz & Metillo, 1998). While this theory has been put forward several times in fish, there is so far no valid evidence of hydrodynamic advantage in travelling schools (Pitcher, 1986). In addition, hydrodynamics could not help fish in unstructured shoaling (or krill in unstructured swarms), so is therefore unlikely to have been a primary reason for the evolution of shoals of fish (or swarms of krill) (Pitcher, 1986). Another assumption in the krill behaviour models of this thesis was that increased swarm density reduced the risk of predation. Pitcher (1986) suggests that the formation of a group itself is unlikely to reduce predation, primarily because the average group member is protected only if the consumption rate of the predator is less when feeding on a group, and secondly because fish shoals are more visible from the air than individuals, which is where a number of predators for both fish and krill initiate their attacks. Hamner (1984) reported that krill schools are likely to be flat in at least one dimension, which is also noted for fish schools, and confers a benefit to group formation from a smaller detection volume (Pitcher, 1986). Further known benefits to schooling come from reduced predation from avoidance, dilution, evasion, confusion, detection, inhibition and prediction, and possible benefits and costs relating to food intake (Pitcher, 1986). Both the benefits and costs of schooling are much better understood in fish than krill, and I suggest further comparisons in this direction would greatly benefit the understanding of krill behaviour in the field.

Is DVM hardwired?

Finally, the causes of diel vertical migration (DVM) in krill are also somewhat of a mystery, despite this being one of their better-documented behaviours. There is a

general understanding among zooplankton scientists that DVM is likely to represent a trade-off between minimising mortality and maximising food intake, one at the cost of the other (Burrows & Tarling, 2004; De Robertis, 2002; Eiane & Parisi, 2001; Gabriel & Thomas, 1988; Clark & Levy, 1988; Iwasa, 1982; Alonzo & Mangel, 2001). The extent, intensity, and patterns of migration in zooplankton may vary within a species by age or size and within season and environmental conditions (Pearre, 1973; Verheye & Field, 1992; Bayly, 1986). However, there is little understanding of how the amplitude or specific pattern of DVM for krill may change in different regions of the Southern Ocean in response to varying conditions of food availability and predation risk. Tarling *et al.* (2002) investigated the causes for midnight sinking in *Calanus finmarchicus*; whether a response to predation or satiation. For krill, most other reports of variations in DVM, for example reverse migration (Kalinowski, 1978; Godlewska, 1996), and daytime surface swarms (Nicol, 2003; Marr, 1962), do not link these to food availability or predation. Given the variation in DVM for krill and other zooplankton species (Pearre, 2003), we might expect DVM to vary in response to changing conditions. However, results from both krill models developed as part of this thesis, particularly for the Scotia Sea, suggest that the DVM of krill in the Southern Ocean is a much more stable strategy than perhaps expected. It is possible that a stable DVM strategy may be the best behavioural adaptation to cope with constantly changing conditions in a challenging environment.

Variability of the Scotia Sea and South Georgia

Both the Scotia Sea and South Georgia are characterised by high variability in food conditions, with generally higher chlorophyll than the rest of the Southern Ocean, particularly at South Georgia. In addition, a long history of exploitation in the region

has caused additional ecosystem imbalance over time. The species that reside here must have evolved to cope not only with the mean level of various variables, such as food availability, but also a broad spectrum of variation (Murphy et al., 1998).

There are a number of ways that krill may be well equipped to deal with variability in the environment. Firstly, krill are actually quite large for a crustacean (Nicol, 1994). The large size of krill may be a factor enabling their powerful swimming ability, aiding a fast escape response from predators, and may also provide a buffer against extended periods in low food conditions. The idea that krill can shrink in response to low food conditions arose from a laboratory experiment by Ikeda and Dixon (1982) where krill survived over 200 days without food, apparently by utilising their structural body protein and by shrinking at each moult. However, whether such a process actually occurs in the field remains debatable given that the extensive field studies of Atkinson et al. (2006) found that krill were able to grow even at very low food levels. Even if krill do not shrink between moults, their large size may mean that they are able to survive for longer in low food conditions, making them better equipped for the variable conditions of the Southern Ocean. This is interesting because growing to a large size seems to be common in Antarctic animals. Others have hypothesised that oxygen availability, increased in cold Antarctic waters, sets the size limit for amphipod crustaceans (Chapelle & Peck, 1999). However, perhaps the ability to cope with a variable and challenging environment is one of the main selecting pressures.

Macaroni penguins have a number of adaptations for living in a variable environment. Firstly, despite laying 2 eggs each year, they nearly always raise one to fledging (Williams, 1981). In addition, the 2 eggs are dimorphic: the first smaller egg is

abandoned while the second larger egg is raised to a chick (Williams, 1981). Within the genus, macaroni penguins show the most extreme intra-clutch egg dimorphism and the greatest disproportionate egg mortality (Williams & Croxall, 1991). The differential egg mortality is an expression of parental investment (Williams, 1980), with macaroni penguins seemingly hardwired to abandon the first egg. Some suggest that this may be an adaptation to ensure successful rearing in a limited time window (Williams & Croxall, 1991). With respect to parental provisioning, there is evidence of a threshold level of prey availability below which parents abandon the chick to feed themselves. In this way, macaroni penguins are able to abandon the current reproduction event in favour of future reproductive events. This is a useful mechanism for a species with multiple breeding events, and has been demonstrated in other species such as kittewakes in Shetland (Hamer et al., 1993). More importantly, the prediction of what the threshold level of food may be, through the use of models such as this, will allow for predictions relating to how the species will respond to variability in the future, such as declines in prey resources through climate change and fishing.

In addition to coping with variability, macaroni penguins have recently had to cope with a decreasing availability of krill. Reasons for an overall decline in the availability of krill to macaroni penguins include the likelihood that krill stocks are currently undergoing a long-term decline (Atkinson et al., 2004) combined with a probable increase in competition for krill from Antarctic fur seals in the region of South Georgia, where fur seal numbers have increased rapidly (Barlow et al., 2002; Trathan & Croxall, 2004) since exploitation ceased in 1907 (Headland, 1984; Bonner, 1968). Fur seals increase the demand on the krill resource as well as possibly out-competing macaroni penguins for both krill and breeding sites. In addition, seals are better equipped to deal

with variability in food sources, because lactating females can draw on their larger body reserves to feed their young (Dall & Boyd, 2004). While the results from this thesis (Chapter 2) suggest that chicks fail when krill availability is low, macaroni penguins have other strategies to cope with low krill availability. As a predator, they are able to switch diet; preying on the amphipod *Themisto gaudichaudii*, although the energetic content is likely to be less and fledging weight may be reduced in these years (Croxall et al., 1999). In addition, macaroni penguins at Heard Island prey mainly on myctophid fish (Green et al., 1998), which are also generally available in the South Georgia area. However, it is unknown on what timescale these penguins can alter their foraging tactics required to change diet.

If the availability of krill to macaroni penguins continues to decline, results from this thesis suggest that the penguins will not breed successfully at South Georgia unless they are able to switch diet. On a local scale, macaroni penguins do worse in unpredictable areas, for example on shelf at South Georgia (Chapter 3), and so recommend that fisheries do not operate in these unpredictable areas, certainly not during the breeding season. Our findings highlight the importance of understanding the effects of both availability and variability in the krill resource on penguin foraging strategies during chick rearing. It also demonstrates that one must consider the life-cycle strategies of penguins in terms of both current and future reproductive success.

Understanding behaviour is important

Experimental and theoretical understanding of animal behaviour has advanced markedly over the last three decades due largely to the development of electronic methods, such as tracking of krill swarms by acoustic monitoring, and satellite tagging of larger

individuals such as penguins and seals. The development of computer models is also an advancement that has added significantly to our understanding of animal behaviour. The 3 models of this thesis demonstrate how computer techniques in combination with experimental data on individual species can help identify key mechanisms that may be of fundamental importance in ecosystems. Models such as these are vital because they enable both the elucidation of weaknesses in the data set and identification of key parameters, as well as predicting how key species might respond to future ecosystem changes brought about by climate change and fishing regimes. Given our history of exploitation and potentially irreversible effects on the atmosphere, these predictions may prove invaluable.

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